

---

# THE EFFECT OF OCEAN ACIDIFICATION ON CALCIFYING FORAMINIFERA

---

Lukas Verboom S-2248719

Bachelor Scriptie

11 July 2014

Supervised by: Prof. Jeanine Olsen, Cees-MarBEE



---

## ABSTRACT

---

Ocean acidification is the anthropogenic change in ocean chemistry driven by the oceanic uptake of chemical inputs in the atmosphere, most importantly that of CO<sub>2</sub>. The increase of CO<sub>2</sub> in the ocean causes the acidity of the ocean to increase, causing the production of calcium carbonate (CaCO<sub>3</sub>) to decrease. Foraminifera are a group of protists that are often protected by a calcite test, and therefore may be hindered by the increasing acidity of the ocean. In this review article I discuss the process of ocean acidification, the adaptations of Foraminifera to low pH conditions and the reaction of Foraminifera to the ongoing ocean acidification. I used the four Representative Concentration Pathways to assess possible future situations. I conclude that compared to other calcifying organisms Foraminifera are likely to survive the ongoing ocean acidification, because they have evolved different strategies to keep their calcite production up. They also produce a form of calcium carbonate that is capable of surviving lower acidities than many other organisms, both in structure and in Magnesium content.

---

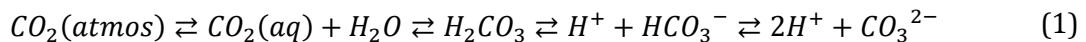
# INTRODUCTION

---

## OCEAN ACIDIFICATION

---

With the use of fossil fuels and global deforestation that started in the Industrial revolution, the CO<sub>2</sub> levels in the atmosphere around the world have increased by about 40% (Solomon et al, 2007). This has had many effects, the most obvious being the increase in air temperature (global warming). However, since the atmospheric CO<sub>2</sub> is in equilibrium with the CO<sub>2</sub> concentration in the oceans, the CO<sub>2</sub> concentration in the oceans is also rapidly increasing, causing another problem. A large portion of the CO<sub>2</sub> emission is taken up by the sea:



The equilibrium between the CO<sub>2</sub> concentration in the atmosphere and the Dissolved Inorganic Carbon (DIC, the sum of the CO<sub>2</sub> (aq), H<sub>2</sub>CO<sub>3</sub>, HCO<sub>3</sub><sup>-</sup> and CO<sub>3</sub><sup>2-</sup>) in seawater is established in approximately one year (Doney et al, 2009). At the current ocean acidity, the DIC in the ocean is usually present in the form of HCO<sub>3</sub><sup>-</sup> + H<sup>+</sup> (Figure 1). This extra Hydrogen ion is a major contributor to ocean acidification. Ocean acidification may be defined as the change in ocean chemistry driven by the oceanic uptake of chemical inputs to the atmosphere, including carbon, nitrogen, and sulfur compounds (Guinotte & Fabry, 2008). In most areas, the carbon compounds are the biggest contributors to ocean acidification, since Nitrogen and Sulphur compounds are often short-lived and are therefore deposited mostly on land (Doney et al, 2007).

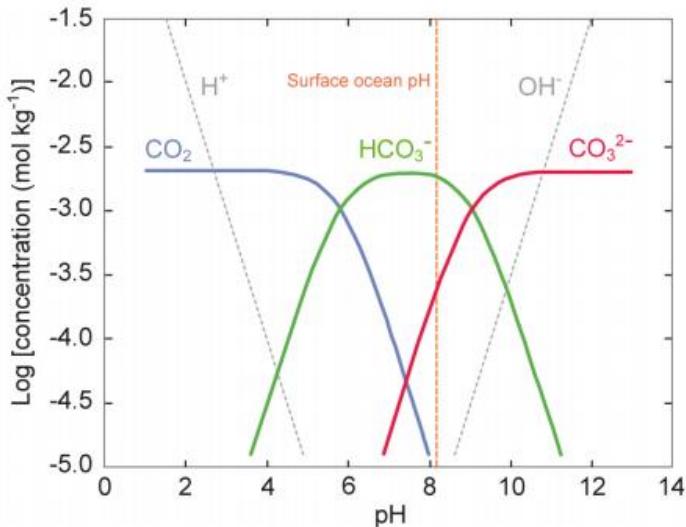


Figure 1. The Bjerrum plot, showing the form in which DIC is present in the ocean at different acidities. The dashed vertical line represents the current ocean acidity (Source: <http://www.nature.com/scitable/knowledge/library/ocean-acidification-25822734>).

The current speed of this process is about 0.02 pH per decade (Royal Society, 2005). The acidity before the Industrial revolution was around 8.21 and has so far decreased to 8.10 (Royal Society, 2005). It is expected to decrease at least another 0.3-0.4 pH with the current CO<sub>2</sub> increase (Orr et al, 2005). Since the pH is the  $-\log_{10}[H^+]$ , the concentration of hydrogen ions in seawater will increase with a factor  $10^{0.3}-10^{0.4} = 2-2.5$ .

## FORAMINIFERA

---

Foraminifera or forams are one of the most numerous and widespread groups of marine protists. As of 2014, 8380 extant species have been recognized (World Foraminifera Database). Most species have a calcareous outer shell, although some naked species exist in fresh water (Pawlowski et al, 1999) and some species use an organic-walled shell (Gooday et al, 2008). The organisms consist of only one cell, but most are colonial and may appear multicellular. Both benthic and planktonic species exist, and both can be found throughout the world's oceans.

Because of the abundance of Foraminifera, they play an important role in the global marine ecosystems. Most species are classed as small heterotrophes, and feed on phytoplankton; however, some species have unicellular algae as endosymbionts which are able to perform photosynthesis (Bernhard & Bowser, 1999). Many animals live mostly on foraminifera, for example sand dollars, marine snails and small fish, some of which have a diet that consists almost solely of foraminifera.

The foraminiferal fixing of calcium carbonate amounts to 25% of the total calcium carbonate production in the oceans (Langer, 2008). The sinking of dead pelagic Foraminifera species is one of the big downward particle fluxes in the open ocean: it is estimated to be about 12% of the total downward particle flux (Silver & Gowing, 1991). Therefore, foraminifera are critical in the ocean chemistry.

The first fossil records of test-bearing Foraminifera were found in Cambrian sediments (Culver, 1991), and it is believed that the first naked Foraminifera have evolved in the late Proterozoic (Wray et al, 1994; Pawlowski et al, 2003). Nowadays benthic foraminifera can be found in almost all marine areas, from the intertidal to the deep ocean and from fresh water to the Dead Sea (Pawlowski et al, 1999; AlmolgiLabin et al, 1995; Gooday et al, 2008; Bergsten, 1994). Planktonic foraminifera live mostly in the top 100 to 200 meter (Mortyn & Charles, 2003). Although most species are aquatic, one terrestrial species has even been found in a tropical rainforest, living in the soil (Meisterfeld et al, 2001).

Together with other protists with a calcareous or siliceous exoskeleton, Foraminifera are often used as a key group for identifying fossil sediments. Because of their small size, microfossils are often better preserved than macrofossils: especially foraminifera can be found in the most eroded sediment layers. The most important information that can be derived from fossil foraminifera in these layers is the ocean temperature at the time of fossilization (Nürnberg et al, 1995). By measuring the  $Mg^{2+}/Ca^{2+}$  ratio in the calcite of their exoskeleton and looking at the species composition the temperature at which the calcite was fixed can be calculated with decent accuracy (Nürnberg et al, 1995).

Furthermore, the Foraminiferal species composition can be used to estimate the age of a fossil layer without the use of radiometric dating methods. The evolution of the important groups of test-bearing foraminifera is well known, and the presence, absence and dominance of species groups (which can be determined by using an electronic or light microscope) is often enough to identify the fossil layer.

The information about sediments is also used to locate fossil fuels. In the 1980's, the expert system Vides (Visual Identification Expert System) was developed by the oil company BP (Athersuch et al, 1994). It allows the user to identify possible petroleum sources by visual examination of the microfossils in the area.

Foraminifera that use a calcareous outer test produce this test by fixating the  $Ca^{2+}$  ion that is abundant in the ocean. However, in fixating this ion, it is dependent on many physical conditions,

most notably the pressure (or depth) and the acidity. In this thesis I will explore the effects of ocean acidification on Foraminifera using the latest climate models and knowledge of Foraminifera, and explore the potential effects of the disappearing of the group on the Benthic ecosystem. Although this paper focuses on acidification, not on global warming, I explicitly take global warming into account where possible because the effects of CO<sub>2</sub> and temperature are intertwined and it would be unrealistic to regard one aspect of climate change in isolation, ignoring the other one.

## METHODS

---

This thesis is based upon a literature review. Articles used in this review paper have been found by using the online search catalogues Web of Science and Google Scholar. In total around 80 articles on ocean acidification, the calcifying process and foraminifera have been examined, most of which from the last decade. The Citation Map option in Web of Science was used to find related articles, both the forward and backward function. Some books on Foraminifera and climate change were used for general information on the subject. I have also used the Fifth assessment of the IPCC for the present state of the changing climate.

Search terms that have been used to find articles on the subject include “Foraminifera + Ocean Acidification”, “Calcification + Foraminifera” and “global warming + calcification”.

## THE PROCESS OF OCEAN ACIDIFICATION AND ITS EFFECT ON FORAMINIFERA

---

The fixation of Calcium by marine organisms is dependent on the acidity of the ocean. When the ocean acidity increases (pH decreases), organisms will have trouble fixing Calcium. Foraminifera depend on Calcium fixation for their growth, and experiments show that their growth will be inhibited with increasing acidity (Haynert et al, 2014; Dias et al, 2010). Some experiments even suggest that with the current increase in atmospheric CO<sub>2</sub>, many calcifying organisms including Foraminifera may be unable to survive the next 100 years because of Calcium deficiency (Orr et al, 2005). Since Foraminifera produce about 1.4 billion tons of calcium carbonate per year, they are one of the biggest calcium carbonate producers in the ocean: it is estimated that they produce almost 25% of the total calcium carbonate production in the ocean (Langer, 2008). Therefore, their disappearance would have significant effects on the chemistry of the world's oceans.

In seawater, calcium is usually present either as a loose ion Ca<sup>2+</sup> or as calcium carbonate CaCO<sub>3</sub>. These two forms are at an equilibrium (after Doney et al, 2009):



The saturation state ( $\Omega$ ) varies with the ionic calcium and carbonate concentrations (after Doney et al, 2009):

$$\Omega = [Ca^{2+}][CO_3^{2-}]/K'_{sp} \quad (3)$$

Where the solubility product K' <sub>sp</sub> depends on the conditions, most importantly on the temperature, salinity and pressure. When  $\Omega < 1$  the CaCO<sub>3</sub> will dissolve, and when  $\Omega > 1$  CaCO<sub>3</sub> can be produced.

The possibility to produce calcium carbonate also depends on the form in which it crystallizes. In the ocean calcium carbonate is produced in two different ways, resulting in two different crystal structures: Aragonite (produced by reef-building corals and some molluscs) and calcite (produced by Foraminifera, Coccolithophores and some molluscs). Of the two, aragonite generally has a lower  $K'_{sp}$  value and is therefore more likely to get a value of  $\Omega < 1$ , the threshold for dissolving.

The  $[Ca^{2+}]$  is usually proportional to the salinity and is therefore not likely to change much (Doney et al, 2009). The  $[CO_3^{2-}]$ , however, is decreasing with the increase of atmospheric  $CO_2$  concentrations, resulting in a decreased  $\Omega$  and therefore an increased dissolution rate of  $CaCO_3$  (Fig. 2). Since the  $K'_{sp}$  decreases with pressure, the formation of both calcite and aragonite is usually limited to a certain depth; this depth decreases with an increase in the atmospheric  $CO_2$  concentration. Therefore, deep water species are predicted to go extinct first because they are unable to fix Calcium and upkeep their shell (Fig. 3).

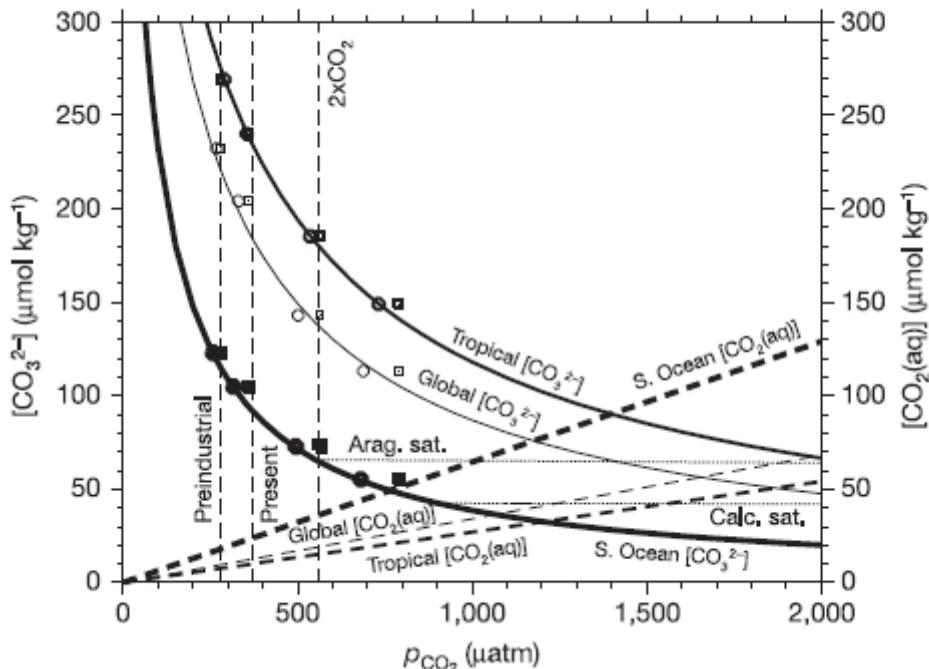


Figure 2. The solid lines show the  $CO_3^{2-}$  concentrations at the surface for different atmospheric  $CO_2$  concentrations for global, tropical and Southern ocean seawater at different atmospheric  $CO_2$  pressure. The dashed lines show the equilibrium between atmospheric and dissolved  $CO_2$  for the global, tropical and Southern ocean seawater. The vertical dotted lines represent the preindustrial (~1830), present (2005) and double industrial  $CO_2$  concentrations. The horizontal dotted lines are the aragonite and calcite equilibrium lines. The vertical distance from a point on the solid line to the calcite equilibrium line is an indication for the effort needed to create calcite. From Orr et al, 2005.

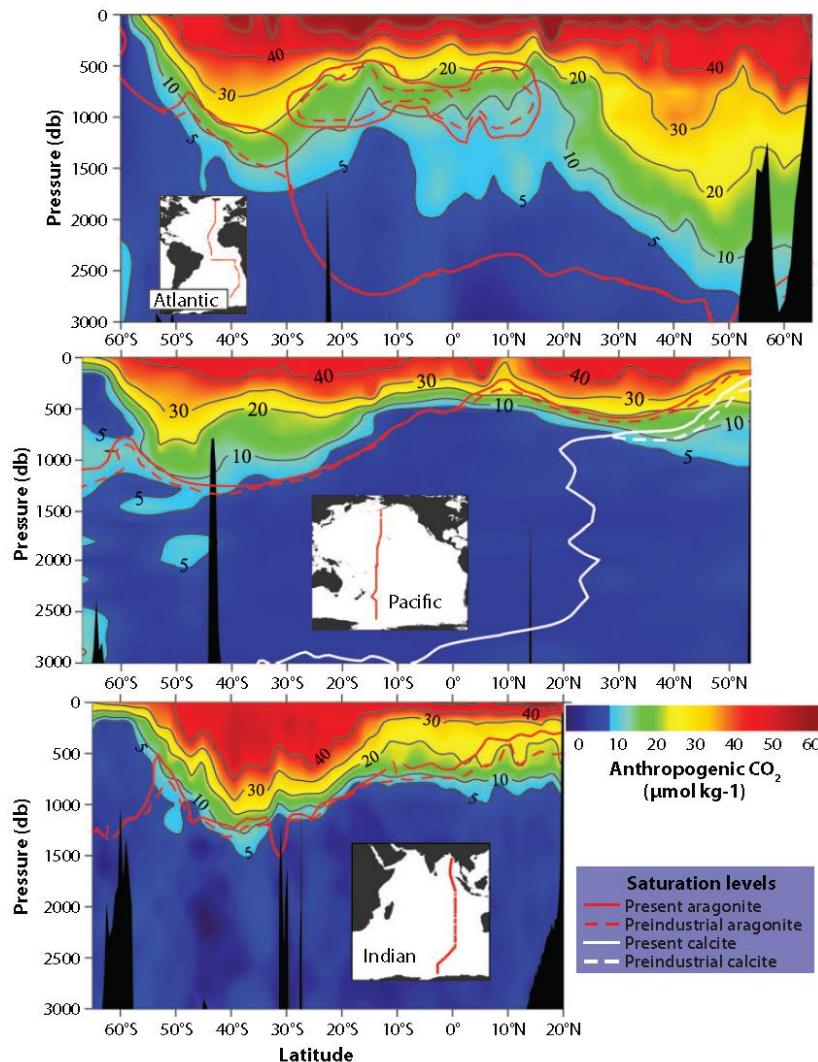


Figure 3. The equilibrium lines (=1) for Argonite (red) and calcite (white) in the three major oceans, on a South-North traject for the Atlantic, Pacific and Indian ocean. Dotted line represents the preindustrial equilibrium line, the solid line the present state. Colors indicate the current anthropogenic CO<sub>2</sub> concentrations. Pressure (db) is an indicator for depth, with 1 bar  $\approx$  10 m. From Doney et al, 2009.

In the evolution of the calcium carbonate skeleton the advantages of the different pathways depended on the Magnesium and Calcium concentrations in the ocean: periods with relatively high Ca<sup>2+</sup> concentrations and low Mg<sup>2+</sup> concentrations have favored organisms that produced calcite, while low Ca<sup>2+</sup> concentrations and high Mg<sup>2+</sup> concentrations favored organisms that produced aragonite (Wilkinson, 1979). However, with the rapidly changing acidity of the ocean, calcite producers like Foraminifera might hold an advantage over aragonite producers again.

## ADAPTATIONS FOR INCREASING THE SATURATION STATE

Over the course of evolution, many Foraminifera groups and species have evolved specific mechanisms that enable them to survive lower ambient acidities and increase their calcite production. In this regard test-bearing Foraminifera can be classified into two paraphyletic, morphological groups (Pawlowski et al, 2013): Miliolid and Hyaline Foraminifera. Miliolids form

needles of calcite, giving a porous surface, while Hyaline Foraminifera produce a porcelaneous test.

## ACTIVELY DECREASING MG<sup>2+</sup> CONCENTRATIONS

The Magnesium ion Mg<sup>2+</sup> is an important inhibitor for calcite production for two reasons. Firstly, the total activity coefficient of CO<sub>3</sub><sup>2-</sup> is reduced in the presence of Mg<sup>2+</sup>, since CO<sub>3</sub><sup>2-</sup> and Mg<sup>2+</sup> form relatively strong ionic bonds in seawater (Zeebe & Sanyal, 2001). This decreases the amount of "free" CO<sub>2</sub> in a solution, on which the production of CaCO<sub>3</sub> depends.

Secondly and most importantly (Zeebe & Sanyal, 2001), the fixation of CaCO<sub>3</sub> will incorporate some MgCO<sub>3</sub> in the crystal structure, because the two molecules have similar structures. This crystal structure with both Calcium carbonate and Magnesium carbonate is much less stable than a crystal structure with only calcium carbonate. Because this effect is so strong, many calcifying organisms including all hyaline Foraminifera and coccolithophorid actively exclude Mg<sup>2+</sup> from their cytoplasm (Wilkinson, 1979; Zeebe & Sanyal, 2001; Ries, 2005). Since membranes are usually impermeable to ions, a low Mg/Ca ratio can be upheld to allow the production of calcite structures almost without magnesium. All planktonic and some benthic Foraminifera have a low Mg/Ca concentration. The mechanism with which Magnesium is excluded from the cell has not yet been demonstrated.

The pH required for calcite production also shows a clear inhibition effect of Mg<sup>2+</sup>. An experimental study performed by Zeebe and Sanyal (2001) demonstrated that at low pressures with a Mg<sup>2+</sup> concentration of 53 mmol kg<sup>-1</sup> a pH of 9.9 is required, while in the absence of Magnesium a pH of 8.2 is required for calcification (Fig. 4). The pH that is required for calcite production when the seawater is depleted of Mg<sup>2+</sup> is approximately the pH of seawater; therefore, the removal of all Mg<sup>2+</sup> from the cell is a potential way of producing calcite.

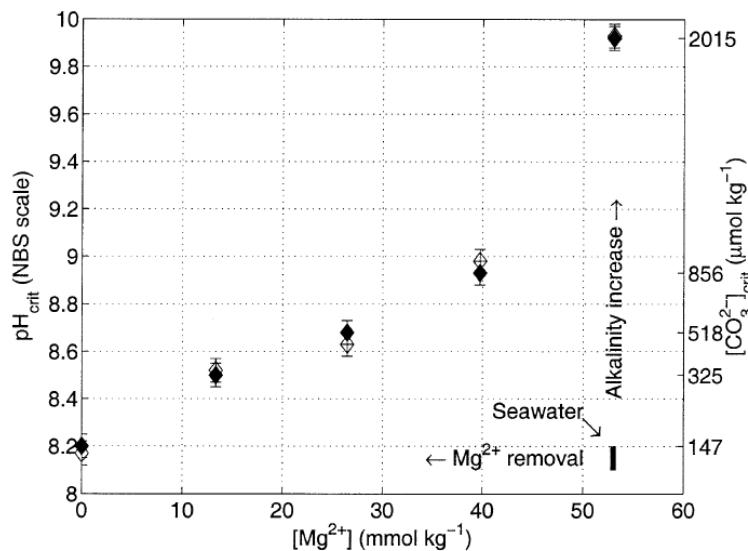


Figure 4. The critical pH values for different Mg<sup>2+</sup> concentrations, defined as the pH at which calcite precipitation could be measured. The different diamonds represent the duplo measurements. The required CO<sub>3</sub><sup>2-</sup> concentrations for calcite precipitation are approximately 13 times higher for a Mg<sup>2+</sup> concentration of 53 mmol kg<sup>-1</sup> than for Mg<sup>2+</sup> depleted seawater. From Zeebe & Sanyal, 2001.

## ALTERING THE ACIDITY IN THE CELL

An alternative approach for increasing the calcite precipitation in the cell is increasing the intracellular pH. De Nooijer et al. (2009) showed that both Miliolid and Hyaline Foraminifera actively remove protons from the cytoplasm to elevate their pH. In this experiment, the pH of living Foraminifera was visualized using a ratiometric fluorescent probe, and it demonstrated how Foraminifera from different groups are able to perform calcification even under high Mg/Ca conditions.

Removing protons from the cell has advantages and disadvantages when compared to the removal of magnesium. The most important advantage is that for an elevation of the pH from 8.0 to 10.0 only approximately 3 mmol kg<sup>-1</sup> H<sup>+</sup> ions have to be removed, compared to the removal of 53 mmol Mg<sup>2+</sup> (the concentration in seawater). Assuming that the transport of one Mg<sup>2+</sup> ion costs approximately twice as much as the transport of one H<sup>+</sup> ion because of the doubled ionic charge (Zeebe & Sanyal, 2001), the cost of reaching the saturation level by increasing the pH is about 53/3=35 times less than by removing the Mg<sup>2+</sup>. However, the cellular membrane is permeable to neutral atoms like H<sub>2</sub>O and CO<sub>2</sub>, and the addition of CO<sub>2</sub> to a medium with a high acidity will cause it to react with water to form calcite and two protons (Equation 1). Therefore the removal of protons is a continuous process.

## PREDICTIONS OF THE LATEST CLIMATE MODELS

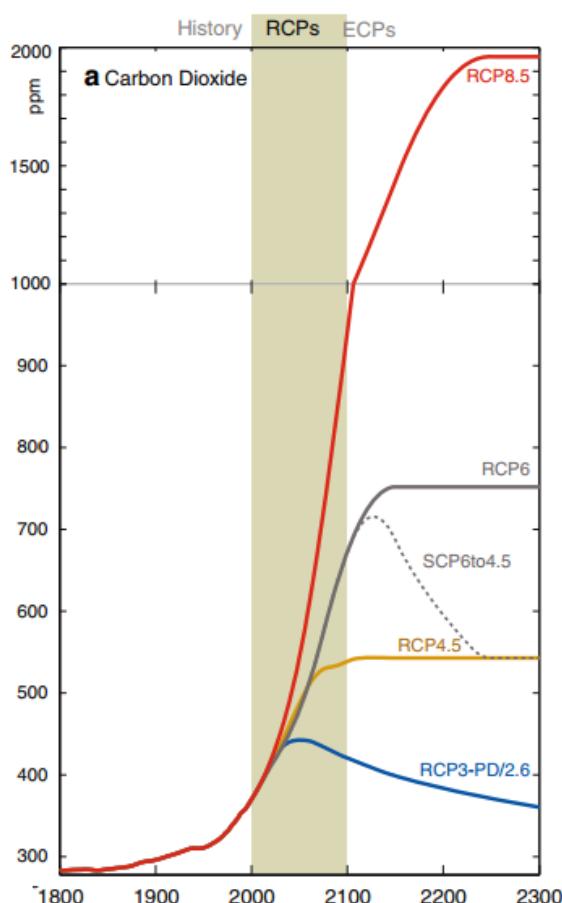


Figure 5. The predicted atmospheric CO<sub>2</sub> over the next 3000 years according to the four Representative Concentration Pathways, the RCP8.5, RCP6, RCP4.5 and RCP2.6. The grey bar represents the 21st century. The red line before 2010 is based on atmospheric measurements. From Meinshausen et al, 2011.

In 2013, the Intergovernmental Panel on Climate Change (IPCC) released the fifth assessment report on climate change under the title Climate Change: The Physical science basis (Stocker et al, 2013). The previous climate report brought out by the IPCC was released in 2007. Here I will discuss the conclusions from the fifth assessment that are important to the topic of this paper. Note that as of June 2014 the atmospheric CO<sub>2</sub> concentration is 401.30 ppm (CO2now.org) and the radiative forcing value is 2.916 W m<sup>-2</sup> (Collins et al, 2013).

In this report, multiple Representative Concentration Pathways or RCP's are used, based on the possible near-future anthropogenic and natural gas emissions. Four RCP models were developed (Moss et al, 2010), the RCP2.6, RCP4.5, RCP6.0, and RCP8.5 model; these are named after the expected radiative forcing values or energy absorbed by the earth's atmosphere by 2100 in W m<sup>-2</sup> (the current radiation is around 3.0 W m<sup>-2</sup>). To model the climate scenarios after 2100 the Extended Concentration Pathways or ECP's are often used; these follow the four RCP models. I will briefly go over each of the RCP models and the consequences on the chemical composition of the ocean.

In the RCP 2.6 model, proposed by the Netherlands Environmental Assessment Agency, the global CO<sub>2</sub> emission reaches its peak within the next two decades (Moss et al, 2010; after Van Vuuren et al, 2007). It is the most optimistic of the models, because with the rapid increase in CO<sub>2</sub> emission a decrease within two decades is unlikely. However, if anthropogenic CO<sub>2</sub> emission decreases within this time frame, a decrease in atmospheric CO<sub>2</sub> is possible, and an equilibrium atmospheric CO<sub>2</sub> concentration of 350 parts per million is predicted – which is about the same as present CO<sub>2</sub> concentration. The deep water ocean acidity will still increase for hundreds of years, since the current equilibrium between atmospheric CO<sub>2</sub> and ocean DIC has not yet reached the deep ocean.

In the RCP 4.5 model, the global CO<sub>2</sub> emission reaches its peak around 2040 because of technological improvements that allow for a reduction in the emission of greenhouse gases (RCP database). The atmospheric CO<sub>2</sub> concentration will reach an equilibrium at around 550 ppm in 2100. This model is considered to be more likely than the RCP 2.6 model. However, since in 66% of the world's countries the CO<sub>2</sub> emission is still growing (world bank group), a lot has to change before this model will be the most accurate. However, if this model proves to be correct, Foraminifera would probably be okay since even in the Southern Ocean the CO<sub>2</sub> levels will get nowhere near the calcite equilibrium line (fig. 3).

The RCP 6.0 model is a stabilization scenario where the CO<sub>2</sub> emission is stabilized after 2100 but will eventually reach an equilibrium by employment of a range of technologies and strategies for reducing greenhouse gas emissions (RCP database). The atmospheric CO<sub>2</sub> concentration will stabilize at around 750 ppm (Meinshausen et al, 2011; fig. 4). In the Southern ocean this may cause problems for the calcifying Foraminifera; the process of calcifying will be much more difficult since the availability of CO<sub>3</sub><sup>2-</sup> will go down rapidly.

The latest and most severe model, the RCP 8.5 model, is the model in which the anthropogenic CO<sub>2</sub> emission keeps increasing with the rate at which it is increasing now (Moss et al, 2010). The CO<sub>2</sub> emission does not reach a peak before 2100 and instead will increase by a factor 4 between 2000 and 2100 (RCP database). This model is sometimes regarded as impossible, since the amount of fossil fuels could not support this amount of emission. It is, however, the direction in which we are going currently with “business as usual” and no drastic mitigation measures.

This model predicts an increase to around 2000 ppm by 2300 (Meinshausen et al, 2011). As a result, the equilibrium line where calcite will dissolve spontaneously will reach the surface in most areas of the world, except for the tropics (Figure 3): for example, the dissolved CO<sub>3</sub><sup>2-</sup> concentration in the Southern Ocean at 2000 ppm atmospheric CO<sub>2</sub> is about 30 µmol kg<sup>-1</sup>, while the equilibrium line is at around 50 µmol kg<sup>-1</sup>. This means that most test-bearing foraminifera around the world will disappear.

## CONCLUSIONS & DISCUSSION

---

The performance of Foraminifera is dependent on the concentrations of Ca<sup>2+</sup> and CO<sub>3</sub><sup>2-</sup> and on the Solubility product K<sub>sp</sub> (Equation 3); the higher the solubility product, the easier it is for Foraminifera to bind Ca<sup>2+</sup> and produce calcite. The value of K<sub>sp</sub>, however, is not constant, and is dependent on the physical conditions, most importantly the temperature, acidity and pressure (see “The process of ocean acidification and its effect on Foraminifera”). The increasing acidity of the ocean that is occurring presently is decreasing the available CO<sub>3</sub><sup>2-</sup> in the ocean. The spontaneous reaction of Ca<sup>2+</sup> and CO<sub>3</sub><sup>2-</sup> is also inhibited by other chemicals in the ocean, among

which the Magnesium ion  $Mg^{2+}$ . The DIC concentrations at the surface can be predicted, because these concentrations follow the  $CO_2$  concentrations in the atmosphere (Doney et al, 2009).

We do not know what climate model or scenario will prove to be the most accurate for predicting the future  $CO_2$  emissions, but we see that three out of four IPCC scenarios show a significant increase in the next century. Since the performance of foraminifera is dependent on the depth, temperature and future  $CO_2$  levels there will always be a threshold below which foraminifera are unable to maintain a calcite skeleton, and the depth of that line will depend on the future atmospheric  $CO_2$  content. Planktonic foraminifera only inhabit the top 100-200 meter of the ocean and therefore will be affected by an increasing pH later than benthic foraminifera.

The RCP climate models that have been used in this thesis allow us to predict the future  $CO_2$  levels, and the measurements by Orr et al. (2005; Fig. 3) allow us to look at the changing availability of  $CO_3^{2-}$  that will follow this  $CO_2$  concentration. Since the difficulty to produce calcite is dependent on the carbonate concentration (Equation 3) and the carbonate concentration is negatively correlated with the atmospheric  $CO_2$  concentration, we can conclude that an increasing atmospheric  $CO_2$  concentration will decrease the production of calcite, and thus affect foraminifera, even if the equilibrium line of  $\Omega=1$  is never reached.

The RCP 2.6 and RCP 8.5 models can be considered the extreme future scenarios; the RCP 2.6 scenario assumes a decrease in  $CO_2$  emission from 2030 and the RCP 8.5 model assumes a steady increase in which policy makers don't intervene: assuming this model is the most accurate for a while, then the adverse effects of climate change should encourage people to search for alternatives. Since the RCP models are not modeled from a socio-economical perspective (Collins et al, 2013) it is hard to conclude from them what feedback the ongoing climate change will have on the anthropogenic emission of greenhouse gases such as  $CO_2$ .

So, concluding that foraminifera will indeed be significantly affected by ocean acidification, can we expect major impacts on our marine ecosystems, and marine foodwebs? Since foraminifera are food to many organisms where they are abundant, their disappearance might result in the disappearance of specific heterotrophes. The benthic foraminifera are often food to benthic filter feeders e.g. benthic fish, sea snails and buried sea urchins, which might decrease with the disappearance of benthic foraminifera. Alternative food for these animals could be diatoms and ciliates; since these groups have a siliceous exoskeleton they will not be affected by the increasing ocean acidity. So based upon the evidence available, I don't expect any major impacts on food webs.

Planktonic foraminifera occur throughout the warmer oceans, but they are often present in smaller densities. As far as I could find, there are no species for which foraminifera are a large part of their diet. Since there is no competition for either carbonate or ionic calcium, the decrease of foraminifera will not result in the increase of other calcium carbonate producing organisms such as coccolithophores and pelagic mollusks (such as sea butterflies and juvenile benthic species). However, since Planktonic foraminifera are responsible for 12% of the downward particle flux, their disappearance could affect the deep sea benthos. Additionally, foraminifera produce almost 25% of the total calcium carbonate worldwide, and a decrease in that will slow down sediment formation in the long run.

As an overall conclusion, I believe that Foraminifera are more resilient to ocean acidification than many other organisms. The group will not go extinct easily, because species have evolved that inhabit the most extreme regions of the earth and have survived the loss of their calcareous exoskeleton. The production of calcite is also more effective than the production of aragonite with an increased ocean acidity under the current chemical conditions of the ocean; therefore, aragonite-producing organisms, such as corals, are likely to disappear first.

Compared to other calcite producing organisms such as many mollusks, Foraminifera are able to handle lower pH conditions because of their ability to exclude magnesium from their calcite shells. Low-Magnesium calcite is not only less likely to dissolve in water, it also allows the Foraminifera to produce calcite under more acid conditions.

## LITERATURE

---

AlmogiLabin, A., SimanTov, R., Rosenfeld, A., Debard, E. (1995). Occurrence and distribution of the foraminifer Ammonia beccarii tepida (Cushman) in water bodies, Recent and Quaternary, of the Dead Sea rift, Israel. *Marine Micropaleontology* **26**: 153-159.

Athersuch, J., Banner, F.T., Higgins, A.C., Howarth, R.J., Swaby, P.A. (1999). The Application of Expert Systems to the Identification and Use of Microfossils in the Petroleum Industry. *Mathematical Geology* **26**: 483-489.

Bergsten, H. (1994). Recent benthic Foraminifera of a transect from the North Pole to the Yermak Plateau, eastern central Arctic Ocean. *Marine Geology* **119**: 251-267.

Bernhard, J. M., Bowser, S.M. (1999). Benthic Foraminifera of dysoxic sediments: chloroplast sequestration and functional morphology. *Earth Science Reviews* **46**: 149–165.

[CO<sub>2</sub> now \(www.co2now.org\)](http://www.co2now.org), consulted 2014/07/08

Collins, M., R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, P. Friedlingstein, X. Gao, W.J. Gutowski, T. Johns, G. Krinner, M. Shongwe, C. Tebaldi, A.J. Weaver and M. Wehner, 2013: Long-term Climate Change: Projections, Commitments and Irreversibility. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G. K Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

Culver, S. J. (1991). Early Cambrian Foraminifera from West Africa. *Science* **254**, 689-691.

De Nooijer, L.J., Toyofuku, T., Kitazato, H. & Stanley, S.M. (2009). Foraminifera Promote Calcification by Elevating Their Intracellular pH. *Proc Nati Acad Sci USA* **106**: 15374-15378.

Dias, B.B., Hart, M.B., Smart, C.W. & Hall-Spencer, J.M. (2010). Modern seawater acidification: the response of Foraminifera to high-CO<sub>2</sub> conditions in the Mediterranean Sea. *Journal of the Geological Society* **167**: 843-846

Doney, S.C., Fabry, V.J., Richard, A.F., Kleypas, J.A. (2009) Ocean Acidification: The Other CO<sub>2</sub> Problem. *Annu. Rev. Marine. Sci.* **2009.1**:169-192.

Doney, S.C., Mahowald, N., Lima, I., Feely, R.A., Mackenzie, F.T., Lamarque, J., Rasch, P.J (2007). The impacts of anthropogenic nitrogen and sulfur deposition on ocean acidification and the inorganic carbon system. *Proc. Natl. Acad. Sci.* **104**: 14580–14585.

Frank, M., Heinz, P. (2013). Impact of elevated pCO<sub>2</sub> on benthic foraminifera from the southwestern Baltic Sea.

Gooday, A.J., Todo, Y., Uematsu, K., Kitazato, H. (2008). New organic-walled Foraminifera (Protista) from the ocean's deepest point, the Challenger Deep (western Pacific Ocean). *Zoological Journal of the Linnean Society* **153**: 399–423.

Guinotte, J.M. & Fabry, V.J. (2008). Ocean Acidification and Its Potential Effects on Marine Ecosystems. *Ann. N.Y. Acad. Sci.* **1134**: 320–342.

Haynert, K., Schönenfeld, J., Schiebel, R., Wilson, B. & Thomsen, J. (2014). Response of benthic Foraminifera to ocean acidification in their natural sediment environment: a long-term culturing experiment. *Biogeosciences* **11**: 1581–1597, 2014

Hofmann, G.E., Barry, J.P., Edmunds, P.J., Gates, R.D., Hutchins, D.A., Klinger, T., Sewell, M.A. (2010). The Effect of Ocean Acidification on Calcifying Organisms in Marine Ecosystems: An Organism-to- Ecosystem Perspective. *Annu. Rev. Ecol. Evol. Syst.* **41**: 127-147.

Langer, M.R. (2008). Assessing the Contribution of Foraminiferan Protists to Global Ocean Carbonate Production. *J. Eukaryot. Microbiol.*, **55**(3): 163–169.

Meinshausen, M., Smith, S.J., Calvin, K., Daniel, J.S., Kainuma, M.L.T., Lamarque, J-F., Matsumoto, K., Montzka, S.A., Raper, S.C.B., Riahi, K., Thomson, A., Velders, G.J.M., Vuuren, D.P.P. van. (2011). The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change* (2011) **109**: 213–241

Meisterfeld, R., Hollzmann, M., Pawlowski, J. (2001). Morphological and Molecular Characterization of a New Terrestrial Allogromiid Species: Edaphoallogromia australica gen. et spec. nov. (Foraminifera) from Northern Queensland (Australia). *Protist* **152**: 185–192.

Mortyn, P. G., Charles, C. D. (2003). Planktonic foraminiferal depth habitat and  $\delta^{18}\text{O}$  calibrations: Plankton tow results from the Atlantic sector of the Southern Ocean. *Paleoceanography* **18**(2): 1037.

Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., van Vuuren, D.P., Carter, T.R., Emori, S., Kainuma, M., Kram, T., Meehl, G.A., Mitchell, J.F.B., Nakicenovic, N., Riahi, K., Smith, S.J., Stouffer, R.J., Thomson, A.M., Weyant, J.P., Wilbanks, T.J. (2010). The next generation of scenarios for climate change research and assessment. *Nature* **463**(7282):747–756

Nürnberg, D., Bijma, J., Hemleben, C. (1995). Assessing the reliability of magnesium in foraminiferal calcite as a proxy for water mass temperatures. *Geochimica et Cosmochimica Acta* **60**(5): 803-814.

Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R.M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R.G., Plattner, G., Dodgers, K.B., Sabine, C.L., Sarmiento, J.L., Schiltzer, R., Slater, R.D., Totterdell, I.J., Weirig, M., Yamanaka, Y., Yool, A. (2005). Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* **437**: 681-686.

Pawlowski, J., Bolivar, I., Fahrni, J. F., de Vargas. C., Bowser, S.S. (1999). Molecular Evidence that Reticulomyxa filosa is a Freshwater Naked Foraminifer. *J. Eukavor. Mirroholi*, **46**: 612-617.

Pawlowski, J., Holzmann, M., Berney, C., Fahrni, J., Gooday, A.J., Cedhagen, T., Habura, A., Bowser, S.S. (2003). The Evolution of Early Foraminifera. *Proc. Natl. Acad. Sci. USA* **100**: 1 1494-11498.

Pawlowski, J., Holzmann, M., Tyszka, J. (2013). New supraordinal classification of Foraminifera: Molecules meet morphology. *Marine Micropaleontology* **100**: 1-10.

RCP Database, 2009. Available at: <http://www.iiasa.ac.at/web-apps/tnt/RcpDb>. Accessed on 07-15-2014.

Ries, J.B. (2005). Aragonite production in calcite seas: effect of seawater Mg/Ca ratio on the calcification and growth of the calcareous alga *Penicillus capitatus*. *Paleobiology* **31**:445–58.

Royal Society (2005). Ocean acidification due to increasing atmospheric carbon dioxide. London: *The Royal Society*, 57 pp.

Silver, M.W., Gowing, M.M. (1991). The "Particle" Flux: Origins and biological components. *Prog. Oceanog.* **26**: 75-113.

Solomon S, Qin D, Manning M, Chen Z, Marquis M, et al. (2007). Climate Change 2007: The Physical Science Basis: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. *New York: Cambridge Univ. Press*.

Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.). (2013). Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. *Cambridge University Press*, Cambridge, United Kingdom and New York, NY, USA.

The World Bank Group: CO<sub>2</sub> emissions (kt).

([http://data.worldbank.org/indicator/EN.ATM.CO2E.KT/countries?order=wbapi\\_data\\_value\\_2010+wbapi\\_data\\_value+wbapi\\_data\\_value-last&sort=desc](http://data.worldbank.org/indicator/EN.ATM.CO2E.KT/countries?order=wbapi_data_value_2010+wbapi_data_value+wbapi_data_value-last&sort=desc)). Accessed on 07-15-2014.

Van Vuuren, D.P., Den Elzen, M.G.J., Lucas, P.L., Eickhout, B., Strengers, B.J., Van Ruijen, B., Wonink, S., Van Houdt, R. (2007). Stabilizing greenhouse gas concentrations at low levels: an assessment of reduction strategies and costs. *Clim. Change* **81**: 119–159.

Wilkinson, B.H. (1979). Biomineralization, paleoceanography, and the evolution of calcareous marine organisms. *Geology* **7**: 524-527.

World Foraminifera Database. World Register of Marine Species (WoRMS)  
<http://www.marinespecies.org/Foraminifera/>

Wray, C.G., Langer, M.R., Desalle, R., Lee, J.J., Lipps, J.H. (1994). Origin of the Foraminifera. *Proc. Natl. Acad. Sci. USA* **92**: 141-145.

Zeebe, R.E., Sanyal, A. (2001). Comparison of two potential strategies of planktonic Foraminifera for house building: Mg<sup>2+</sup> or H<sup>+</sup> removal? *Geochimica et Cosmochimica Acta* **66**: 1159-1169.