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Interactive comment on "Coccolithophores on the north-west European shelf: calcification rates and environmental controls" *by* A. J. Poulton et al.

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Anonymous Referee #1

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Response: We would like to thank each of the three reviewers for their comments and have responded to each point raised below.

The manuscript 'Coccolithophores on the north-west European shelf: calcification rates and environmental controls' presents an extensive data set including in-situ measurements and manipulative incubation experiments. The focus is on the response of coccolithophores to environmental conditions such as nutrient availability and carbonate chemistry speciation. The manuscript is generally well written, the conclusions, how-

ever, are vague and interpretation of the manipulative experiments are, in my opinion, problematic (see below).

Response: A lack of clear focus for the abstract and conclusions was a common comment across the three reviews and we have now rewritten these sections to highlight the main findings of the study (i.e., strong in situ relationships to light and not nutrient and carbonate chemistry; strong response to nutrient addition in the shelf E. huxleyi dominated communities but not in the oceanic mixed species community; depression of growth rates in elevated pCO2 treatments in two of the bioassays as well as changes in cellular levels of calcification. We will respond to comments on the interpretation of the manipulation experiments in the relevant sections.

General comments and suggestions: 1: It seems that most calcification related data, such as coccolith calcite or cell specific calcification, is based on the dominant species Emiliania huxleyi. Given a contribution of up to 30% by other coccolithophores than Emiliania huxleyi (page 2702), what are the associated uncertainties?

Response: Cell-specific calcification (cell-CF) is not based on the dominant species, E. huxleyi, but is calculated simply by dividing community calcite production (CP) by coccolithophore cell abundance (for all species). Only values for E. huxleyi cell-CF are common in the literature, and hence we have a better idea of the range of values possible by E. huxleyi dominated communities than more mixed populations. We have made this point several times in the present manuscript, and in previously published material (Poulton et al., 2010, 2013; Charalampopoulou et al., 2011) and are careful not to over interpret patterns in cell-CF when E. huxleyi is not dominant. The first version of the paper did lack information on the species composition in the experimental bioassays, which we have now rectified and shows that the first bioassay had a mixed community of E. huxleyi and G. muellerae whereas the other two communities were mono-specific and dominated by E. huxleyi.

2: Using the data on pH from table 1 and of Emiliania huxleyi dominance from table

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3, I wasn't able to verify 'a significant ($p < 0.01$) inverse correlation between pHT and E. huxleyi dominance' (page 2712). I would suggest to show all statistically significant correlations in a separate graph. In this respect it was confusing that in the results section 'E. huxleyi abundance was negatively correlated to ' while in the discussion 'the only one relationship to a parameter of the carbonate chemistry' was the one mentioned above (pH and E. huxleyi dominance).

Response: Apologies, this was our mistake – the Results present a correlation between saturation state, whereas the discussion mistakenly reported this as a correlation with pHT. No correlations were observed with pHT. There are 22 statistically significant correlations, through a combination of stations examined and not examined, meaning that plotting these correlations is difficult. However, we acknowledge that this part of the manuscript needed greater clarity and have addressed this in the revised version with a new Table (see pdf supplement) which includes the correlations for (now) four different sets of sites: All, Stratified only, E huxleyi dominated, and (new) E huxleyi dominated without the Helgoland site. This new table allows us to better focus in the relevant text on how the environmental drivers were influencing coccolithophore dynamics across the different sites. Specifically, we now conclude that light availability, as indicated by relationships between CP and mixed layer average irradiance (Ed[ML]) and cell-CF and incidental irradiance (Ed[E0+]), has a strong influence on coccolithophore calcification in shelf waters.

3: The title suggests that there are new insights into environmental control on coccolithophorid calcification rates/abundances and several significant correlations are presented in the results. In the discussion, however, no clear conclusions are drawn with this respect, although it is highlighted that 'no co-variability of pH/ was observed with other growth limiting factors' which 'is key to interpreting coccolithophore ecophysiology in relation to growth-limiting factors and needs to be carefully considered in future studies'. Why not exploring this further in this study?

Response: We have now rewritten the abstract and conclusions, as well as the sec-

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tion relating environmental factors to coccolithophore dynamics, to highlight the major findings of our study (see response to general comment). We have also rewritten the cryptic comments the reviewer eluded to above to make the message simple – "This contrast in coccolithophore response to pH/saturation state, between gradients where carbonate chemistry co-varies with other environmental parameters and gradients where there is no co-variability, implies that any correlation between pH/saturation state and coccolithophore dynamics along environmental gradients should be viewed with caution and in the context of any naturally occurring co-correlation with nutrient and light availability."

4: For the incubation experiments I would have liked to see data on initial cell numbers and calcification rates to compare with final ones. Looking at the nutrient data (phosphate and nitrate) it seems that hardly anything was utilized in the high CO2, in sharp contrast to the ambient treatments, even when nitrate and phosphate were added but also in the controls without additional nutrient addition. The only exception is the high CO2+NP treatment were there was at least some nitrate consumption although also considerably less than in the ambient+NP treatment. The lack of significant nutrient utilization in all elevated CO2 treatments is also reflected in the lack of significant chlorophyll build-up during the two days of incubation, again in contrast to the ambient ones. Thus, it seems that community calcification rates at elevated CO2 did not decrease but rather that community calcification rates at ambient CO2 increased. The communities at elevated CO2 just did not grow, which is strange. However, this could well be a stress related response to the acid/NaHCO3 addition, leading to an extensive lag phase with no growth. Thus, the short-term bioassays do not seem suitable to infer physiological responses to ocean acidification. This potential issue should also be considered for the accompanying paper by Richier et al.

Response: Firstly, the initial cell numbers and initial rates of CP (and cell-CF) are presented in Figure 7 (dashed line), allowing the calculation of growth rates and comparisons across treatments. From this it is clear that the coccolithophore communities

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in all three bioassays always had positive growth rates. Secondly, comparison of the dashed lines in Fig. 7 and the T48 measurements highlights that: (i) all bioassays had a positive and relatively high (net) growth rates (pg 2714, lns 9-11), ranging from 0.2-0.7 d-1, with growth rates in bioassays 4B and 5B similar across treatments (0.2-0.7 d-1); and (ii) elevated pCO2 did depress the coccolithophore growth rates. I am not sure why the reviewer considers this response (i.e. a reduced growth rate) to environmental stress as strange – there is no evidence available to consider whether such depressions occur over the short-term in longer term experiments (e.g., mesocosms) during the 'acclimation' period. Moreover, it is well known that physiological responses of marine phytoplankton vary with culturing method, nutrient limitation and acclimation time (Hennon et al., 2014) and thus multiple physiological responses of phytoplankton can be obtained under experimentally increased CO2 with little consensus on magnitude or direction (Riebesell et al. 2007; Kim et al. 2011 and Engel et al. 2008). The decrease in growth rate observed at high pCO2 is most likely due to the acid/NaHCO3 addition (i.e. pH change) and could indeed result in the increase of the lag phase in the experimental bottles. However the direct impact of acid addition on phytoplankton physiology is strongly suggested, as the responses obtained were not homogenous but rather specific. Indeed, size- and taxonomy-related responses to change in pCO2 in both main (Richier et al. 2014) and additional experiment (this paper) were observed. Lastly, we never state that "the short-term bioassays are suitable to infer physiological responses to ocean acidification" but rather that "the bioassays tested coccolithophore sensitivity to sharp changes in carbonate chemistry rather than acclimation to ocean acidification processes occurring over decades per se." (pg 2713, lns 9-11).

Engel A, Schulz KG, Riebesell U, Bellerby R, Delille B, Schartau M. 2008. Effects of CO2 on particle size distribution and phytoplankton abundance during a mesocosm bloom experiment (PeECE II). Biogeosciences 5:509–21.

Hennon GMM, Quay P, Morales RL, Swanson LM, Armbrust EV. 2014. Acclimation conditions modify physiological response of the diatom Thalassiosira pseudonanna to

elevated CO2 concentrations in a nitrate-limited chemostat. J Phycol 50, 243-253.

Kim JM, Lee K, Shin K, Yang EJ, Engel A, Karl DM & Kim HC. 2011. Shifts in biogenic carbon flow from particulate to dissolved forms under high carbon dioxide and warm ocean conditions. Geophys Res Lett 38:1–5.

Riebesell U, Schulz KG, Bellerby R, Botros M, Fritsche P, Meyerhofer M, Neill C, Nondal G, Oschlies A, Wohlers J & Zollner E 2007. Enhanced biological carbon consumption in a high CO2 ocean. Nature 450:545–8.

Specific comments: 1: P.2687, L.20 Here a correlation is described which is not necessarily the actual cause.

Response: Abstract completely rewritten and correlations described as indicating rather than causal.

2: P.2688, L.7 There are many coccolithophores significantly larger than 10μm.

Response: Indeed, sentence changed to read “Many coccolithophore species (e.g. Emiliania huxleyi, Gephyrocapsa muellerae) have cell diameters of 5-10 um, making them a potentially important component of the nanoflagellate (herein < 10 um) community.”.

3: P.2688, L.18 The author’s could also include the Sarsia paper by Egge et al. (1994) for the influence of nutrient availability on coccolithophore blooms. If I remember correctly, this paper identified rather high nitrate to phosphorus conditions favorable for blooms than low nitrate to phosphorous as speculated on the first line of the following page.

Response: The review by Merico and Tyrrell (2004) discusses the Egge and Heimdal (1994) paper based on mesocosm experiments of different N:P ratios and absolute amounts in considerable detail, as well as the other factors linked to coccolithophore blooms. Hence, we have not included much of the primary literature in this section.

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Egge JK, Heimdal BR. 1994. Blooms of phytoplankton including Emiliania huxleyi (Haptophyta). Effects of nutrient supply in different N:P ratios. Sarsia 79, 333-348.

4: P.2690, L.1 It should read '< 2μm'.

Response: Corrected.

5: P.2690, L.5 Which effect?

Response: Rephrased to say; "The effects of global environmental change (e.g., increased temperature and stratification, deoxygenation)...".

6: P.2691, L.3 Light profiles were taken for the pre-dawn stations, i.e. during the night?

Response: Light profiles were made during dawn, before sunrise. Although absolute light levels were low, there was enough light for the PAR sensor to calculate a vertical attenuation coefficient and estimate the light depths. We have rephrased parts of the revised paper to take account of this.

7: P.2694, L.17 I would suggest to rather cite the original Welschmeyer paper here.

Response: The Welschmeyer (1994) paper describes the optical configuration of the fluorometer rather than the filtration and extraction method used (which is described in Poulton et al. 2010).

Welschmeyer NA. 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and phaeopigments. Limnol. Oceanog. 39, 1985-1992.

8: P.2696, L.13 What was the rational to always add silicate together nitrate or phosphorus?

Response: Silicic acid was added to ensure that diatoms were not nutrient limited – i.e., the experiments were not designed to test differential nutrient effects on the community. We have now noted this in the relevant methods section.

9: P.2703, L.12 A coccolith production rate of eight per hour is clearly too high for

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Emiliania huxleyi.

Response: Indeed, but we do not state that it is E huxleyi doing this but note that this station has other species with higher cellular calcite levels present (pg 2703, 11-14). However, in the revised version of the paper we have removed sections on coccolith calcite content and coccolith production as this is covered in more detail in Young et al. (2014).

10: P.2710, L.3 Light availability should also affect primary production. Was this the case here?

Response: Yes (e.g., total primary production correlated with incidental PAR ($r = 0.61$, $p < 0.05$)), and we already mention that vertical profiles of PP showed decreases with depth and irradiance (pg 2700, lns 19-21). However the focus of the paper is on the environmental factors influencing coccolithophore calcification and so we have not gone into huge detail here.

11: P.2710, L.8 Why and how did mixed layer irradiance influenced community size and CP, while water column structure had a n influence on cellular calcification? Also, a correlation should not be confused with an cause/effect relationship.

Response: Indeed, a correlation does not mean causation and this is why we used terminology such as 'appeared to influence' rather than stronger ones such as 'directly influenced'. The point we were making here was that bulk community CP and coccolithophore cellular abundance only correlated with mixed layer average irradiance (Ed[ML]) whilst cell-CF correlated with incidental irradiance (Ed[0+]). We have now rewritten this section of the results and discussion to only highlight the fact the CP and cell-CF were both correlated with light availability and no correlations with nutrient availability were found (if we exclude the Helgoland site).

12: P.2712, L.8 Coccolithophores have probably a bigger effect on pH than pH on coccolithophores.

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Response: This is an intriguing statement, and surely true in a high biomass batch culture where balances between photosynthesis, calcification and respiration control the dissolved stocks of carbon and ions. However, in natural communities where coccolithophores make <5% of the total population, then the marine community has a bigger effect on pH. It is not clear exactly what point the reviewer is trying to make with this statement.

13: P.2715, L.6 and P.2716, L. 22 It seems that there was no negative but rather no response to decreasing pH (see also comment above).

Response: As shown in Figure 7A and 7B, community CP was significantly lower in the elevated pCO2/lowered pH experiments – a negative response (i.e., they didn't increase in response to lowered pH). These were due to lower growth rates in the elevated pCO2 treatments, although the growth rates were still positive (Fig. 7).

Interactive comment on Biogeosciences Discuss., 11, 2685, 2014.