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Interactive comment on "A niche comparison of *Emiliania huxleyi* and *Gephyrocapsa oceanica* and potential effects of climate change" *by* Natasha A. Gafar and Kai G. Schulz

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-Abstract: -As I understand it, the inhibitory effect of increasing CO2 on G. oceanica is the main reason for this species' projected contraction under a future scenario. This should be emphasized in the abstract (1). As it is now, the projection of a contracted G. oceanica niche is surprising because it is generally the warmer water adapted species. Also, since E. huxleyi CCPP shows a better correlation with satellite-derived PIC than when combine with G. oceanica, this should be mentioned in the abstract (2). Otherwise, given the title of the paper, one assumes that the CCPP estimates are derived from partitioning niches between E. huxleyi and G. oceanica. Also, maybe a sentence

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at the beginning of Abstract describing why these two particular species are being compared would be helpful.

1. We will modify to “For a future RCP 8.5 climate change scenario (1000 μatm fCO2 and + 4.8C) we project a primarily CO2 driven niche contraction for G. oceanica to regions of even higher temperatures.” 2. We will modify to “CCPP estimates were based on E. huxleyi alone as interestingly there was a better correlation with satellite-derived PIC than when in combination with CCPP for G. oceanica. Excluding the Antarctic province from the analysis we found a good correlation between CCPP and satellite derived PIC in the other regions with an R2 of 0.73 for Austral winter/Boreal summer and 0.85 for Austral summer/Boreal winter.” 3. We will modify the beginning of the abstract to “Based on our analysis of the two most common coccolithophores in today’s ocean. . .”

-Intro: -Page 2, lines 3-9: This paragraph on future changes to the surface ocean environment needs expanding. What happens to nutrient availability with increasing stratification (1)? How could this affect CaCO3 production and growth rate in coccolithophores (2)? How could increasing CO2 affect growth rate/ calcification of coccolithophores (3)? The impact of increasing light is described but not the other effects of climate change. Increasing temperature would also increase metabolic rates, unless nutrient limitation becomes too strong. Overall this paragraph just needs more development with respect to the effects of anthropogenic climate change on coccolithophore habitat and how each effect could impact growth/calcification.

-The potential effects of CO2 on phytoplankton in general and coccolithophores in particular are already covered in the previous and following paragraph. Nevertheless, we will modify the text to “Depending on emission scenarios, ocean temperatures are projected to increase from 2.6 to 4.8C by 2100 (IPCC, 2013b). In addition, warming of the ocean is expected to enhance vertical stratification of the water column, resulting in a shoaling of the surface mixed layer and increasing overall light and decreasing nutrient availability in the euphotic zone (Bopp et al., 2001; Rost and Riebesell, 2004; Lefebvre et al., 2012). While increased light intensity and temperatures often accelerate growth in phytoplankton, excessive levels of light and temperature can cause damage to the photosynthetic apparatus and reduce effectiveness of enzymes thus decreasing growth (Powles, 1984; Rhodes et al. 1995; Crafts-Brandner 2000; Zondervan et al., 2002; Helm et al., 2007; Reviewed in Pörtner and Farrell, 2008). Meanwhile, reduced nutrient availability could diminish overall productivity."

-Page 2âĹijline 18: There needs to be a paragraph with some background about the two species discussed in this paper. Why are you comparing these two particular coccolithophore species? These are the two major bloom forming coccolithophores. It is well known that E. huxleyi is very widespread, but how abundant is G. oceanica? Where does G. oceanic tend to thrive? Also mention that there are several different mophotypes of E. huxleyi and how they might differ. A bit of biogeography background would be helpful. This would then lead into the fundamental vs. realized niche paragraph.

-We will add the following text in line 14 after "(Rost and Riebesell, 2004; Broecker and Clark, 2009; Poulton et al., 2007, 2010)." The coccolithophores Emiliania huxleyi and Gephyrocapsa oceanica are considered the most common species in present day coccolithophore communities. E. huxleyi is a ubiquitous coccolithophore species having being observed from polar to equatorial regions, nutrient poor ocean gyres to nutrient rich upwelling systems, and from the bright sea surface down to 200m depth (McIntyre & Be 1967; Winter et al. 1994; Hagino & Okada 2006; Boeckel & Baumann 2008; Mohan et al. 2008; Henderiks et al. 2012). The wide tolerance of E. huxleyi to different environmental conditions is believed to be, at least partially, explained by the existence of a number of environmentally selected ecotypes and morphotypes within the species (Paasche 2001; Cook et al. 2011). G. oceanica is also found in most oceanographic regions (McIntyre and Be 1967; Okada and Honjo 1975; Roth and Coulbourn 1982; Knappertsbusch et al. 1993; Eynaud et al., 1999; Andruleit et al. 2003; Saaveda-Pellitero et al. 2010), however with a tendency towards warmer waters with very few specimens observed below 13oC (McIntyre and Bé, 1967; Eynaud et al., 1999; Hagino et al., 2005).

-Page 2 lines 28-35: the CCPP- PIC comparison is left out of this paragraph. It would be good to mention this here to indicate how it ties in with the E. hux – G. oceanic niche comparison.

We will add the following to the end of the paragraph "Finally, we compare satellite derived particulate inorganic carbon estimates with a recently proposed metric for coccolithophore success on the community level (Gafar et al. 2018), i.e. the temperature, light and carbonate chemistry speciation dependent calcium carbonate potential.

-Methods: -Page 3, line 4: Why test such high CO2 values? Are these even realistic? For instance, if end of the century CO2 concentration of 985μatm (about 50μmol kg-1 aqueousCO2), corresponds to a 4.8 deg C temperature increase, then why go up to 250μmol kg-1 CO2? The range of CO2 is therefore bigger than the temperature range in terms of real world conditions. An explanation for this experimental setup would be helpful.

Fitting non-linear responses of multiple stressors to data requires a broad range of environmental conditions, as otherwise the shaping factors of limitation and inhibition are lost (absent from data while present in model equation). With this broader range we also have the added benefit for identifying tipping points and changes in sensitivities to CO2 with changing light and temperature.

We will make our rational more clear in the methods section by adding the following to Page 3 line 3: "To accurately identify optimal conditions, tipping points and sensitivities of rates in response to changing CO2, light and temperature, a broad range of experimental conditions were required. Mono-specific. . .. . .."

-Page 3, section 2.1: The authors need to mention the particular E. hux morphotype being tested (PML B92/11 is morphotype A).

We will add the requested information.

-Page 4, line 22: Why would there be a lag phase? It seems the growth rate is calculated correctly (after the lag phase is over), but a quick explanation of why there is a lag phase at extreme CO2 and whether this is a normal phenomenon in phytoplankton culturing and physiological testing would be helpful.

-At both, the extreme low and high CO2 treatments, carbonate chemistry at the end of the pre-incubation phase can significantly deviate from initial and hence experimental treatment conditions due to enhanced air/water CO2 gas exchange during regular cell abundance monitoring. This in turn can induce a lag phase at the beginning of experimental conditions as observed here. We will add this information to the method's section.

-Page 5, section 2.7: I find this section about the data transformation confusing, particularly about the temperature. Is this just for growth rate? How do the resulting temperature-dependent growth rates compare to other studies on coccolithophores (Fielding 2013, Buitenhuis et al., 2008)?

This transform is applied to all rates to reduce skew and are common practice in multivariate fitting procedures.

As mentioned within section 2.7, this temperature transform compares well to other temperature dependant growth rate equations such as the single species responses to the Eppley temperature envelope curve and the Norberg model. Our temperature-dependant growth rate estimates show a similar response to the optimal growth function in Buitenhuis et al. 2008 and the Flinn equation in Fielding et al. 2013. The power function in Fielding et al. 2013 also follows a similar pattern, of growth rate increase with rising temperature, as our transform but lacks a term to inhibit rates as temperatures rise above optimum.

However, our temperature transform results in a much stronger decrease in/inhibition of growth rates above and below optimum temperatures than is observed for any of the above equations. This feature was chosen by us as it is backed up by response data from multiple E. huxleyi strains in Zhang et al. 2014 Between- and within-population variations in thermal reaction norms of the coccolithophore Emiliania huxleyi Limnology and Oceanography, 59(5), 1570–1580.

-Page 7, line 4: Unneeded commas before and after “relatively simple”...or just rewrite for clarity “As such we wanted to examine how projections of productivity using our relatively simple equation compared to coccolithophorid productivity patterns observed in natural systems”

We will adopt this suggestion.

-Page 7, line 13: A citation of the CCPP metric is needed.

We will adopt this suggestion.

-Page 8, line 14: Need citation for the PIC:POC ratios used for E. huxelyi and G. oceanica

This has been corrected as detailed in the response to reviewer 1.

-Page 8, last paragraph: I took me awhile to figure out the CCPP estimates were made in three ways: 1) just E. huxleyi 2) just G. oceania 3) both species combined Is this correct? Only results for E. huxleyi CCPP was presented so maybe clarify here that only the results with the highest correlation to satellite PIC are shown. It’s confusing because there are details described in the previous paragraphs about deriving CCPP for each species but then the results only show E. huxleyi CCPP.

Yes, the estimates were made using just E. huxleyi, just G. oceanica and then both species combined. Only results for E. huxleyi were presented as G. oceanica alone and in combination with E. huxleyi did not provide as good a correlation to satellite PIC. We shall mention at the end of this method section “While three CCPP scenarios are presented above, only the results with the highest correlation to satellite PIC are shown and discussed below.”

-Page 8, lines 26 and 27: Need parentheses around year for citations Gregg and Casey (2007) and Longhurst (2007).

We will adopt this suggestion.

-Results: -Page 9, Results section in general: Please specify in the headings that these are only the results for E. huxleyi (not G. oceanica).

We will adopt this suggestion (i.e. Change to “E. huxleyi responses to . . ..” for sections 3.1, 3.2 and 3.3).

-Page 9, line 2: Perhaps develop this small section a bit more. Which rate showed the best fit?

We will change the sentence to “The fit equation (Eq. 2) was able to explain up to 85% of growth, 80% of calcification and 73% of photosynthetic rate variability in E. huxleyi across a broad range of carbonate chemistry (25-4000 μatm), light (50-1200 μmol photons m-2s-1) and temperature (10-20oC) conditions (Table 1).”

-Page 9, line 6: Instead of just saying “all rates”, please remind the reader what metabolic rates you are examining and refer to the equation presented in the methods.

We will change the sentence to “Based on fits of equation 2, growth, calcification and photosynthetic carbon fixation rates all had. . .. . .”

-Page 9, line 7: It’s hard to understand exactly what to look at in Table 2 and 3 to support this sentence (2nd sentence of the paragraph). It seems like CO2 concentrations of K1/2sat range form 0.85 to almost 5μmol kg-1 depending on light and temperature...

The difference in K1/2 sat concentration between treatments is not what is important here. Rather it is the difference in K1/2 sat between the different processes for the same conditions that supports this sentence. Under all conditions the difference in

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CO2 concentration, between the three processes, required to support half of maximum rates is less than 1-2 μmol kg-1. We will clarify this issue in the revision.

-Page 9, lines 8-10: Mention what are the optimal CO2 concentrations and put this into units of μatm to make it more relatable to the reader. Are we at the optimum CO2 already for coccolithophores or will it come in the near future? At what CO2 concentrations is K1/2inhib reached? More specifics would give the reader more useful information.

We will add the CO2 concentrations for optima and K1/2 inhib. The reason we use CO2 concentrations rather than fugacities is that for the same concentrations, the fugacity would be different for two temperatures.

-Page 9, line 14/15: What columns in table 2 are the reader supposed to be looking at? Are you referring to the Vmax column?

Yes. The Vmax not only represents the maximum rate in a treatment, but also is where we see the greatest change in rates due to temperature and light. This is because Vmax is achieved under optimal CO2 conditions and, based on our findings, rates under optimal CO2 conditions are the ones which are most sensitive to changes in temperature and light conditions.

-Page 9, line 18: I had to read this sentence several times before I actually understood it. Would this be a better way to put this?: "CO2 half saturation concentration were insensitive to temperature. However, under increasing temperatures CO2 optima for growth and inhibition occurred at lower CO2 concentrations"

Yes, with some modification. Changed to "CO2 half saturation concentrations were insensitive to temperature (Table 2). However, under increasing temperatures CO2 concentrations for both optimal growth and for inhibition of rates to half the maximum (K1/2CO2 inhib) decreased (Table 2)."

-Discussion: -Page 10, line 6: Since this is a major conclusion of the paper, it should be shown directly somehow. All the original G. oceanica data is published elsewhere, so a graphical summary of BOTH the E. hux and G. oceanic data would be helpful. This could be done through line plots comparing the metabolic rates of the two species under varying CO_2 or in a bar plot comparing the rates. I just think it's necessary to show a visual comparison of E hux and G oceanica data (or data-derived function) since the title of the paper indicates a comparison.

Actually, the data for the response of G. oceanica to CO_2 under different light conditions is already presented for easy comparison in a supplementary table. We will add this cross-reference into the paper. This table is already referenced multiple times in the paper and we do not wish to repeat information by also presenting it in graphic form.

The data for the response of G. oceanica to CO_2 under different temperatures is the only data not available for direct comparison to E. huxleyi in this paper and we feel it does not add enough to this paper to be included here as well. Besides this the main focus of the comparison between the species for this paper is in the fundamental and realised niche descriptions.

-Page 10, line 30: A change in CO_2 optima of 11μmol kg-1 is not that small.

We will change the sentence to "Changes in temperature produced little (<1 μmolkg-1) change in CO_2 substrate half-saturation ($K_{1/2CO_2\ sat}$) levels, at least within the measured range (Figure 1, Table 2). CO_2 requirements for optimum rates had a tendency to slightly decrease with warming temperatures. Similar results were observed for.. . . . ."

-Page 11, line 5: Unneeded commas around "at least some"

We will change this.

-Page 11, line 15: Again, here is where a comparison figure between E. hux and G. oceanica would be helpful.

All information is available in the accompanying tables.

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-Page 12, line 3: The range tested in this study is so much higher than even what projected under RCP8.5 at the end of the century. The temperature range tested in this study is much more realistic. How warm would the world be under 5000μatm CO_2?

Please see our response to the comment on Page 3.

-Page 12, line 12: I think a major limitation of this study is the focus on just one strain of one morphotype of E. huxleyi. Different E. huxelyi morphotypes show significant genetic and physiological variability (see Read et al., 2013; Langer et al., 2009; Krumhardt et al., 2017). Accounting for these differences could add significant uncertainty to the conclusions. I think that the last sentence of section 4.4 (before section 4.4.1) would fit better in a section on the "Limitations of this study" at the end of the Discussion section, where you describe how E huxleyi strain PML B92/11 is used to be representative of all E. huxleyi for determining niche and projections under future CO_2 and warming in this study. This doesn't make the results invalid, but is just a limitation that needs to be made clearer. This would then lead in nicely with the conclusion that more testing with colder water strain/species/morphotypes of E huxleyi is necessary.

Please refer to our reply to the first comment of reviewer one for our response on the limitations of using a single strain. In terms of creating a limitations section, we believe it makes it easier to follow the paper, and remind readers of its limitations, if we mention the specific limitations of our research not as a separate section but rather as part of the discussion for each section. In this way it can be made more clear what the limitations are and what they mean for each section.

-Page 12, line 22: Capitalize "Figure"

We will change this.

-Page 13, line 7: I think it's well established that E. huxleyi is a generalist, given its widespread distribution from subpolar to tropics.

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We will change to “indicating that this species is more of a generalist than G. oceanica”.

-Page 13, line 9: Unneeded comma after “niche”

This will be removed.

-Page 13, line 25: Reference needed for this E. huxleyi warm water strain that outcompete G. oceanica at temps > 25C

This observation is based on the data compiled in figure 6. The data sources will be referenced in the figure caption.

-Page 13, line 32/33: I’m confused by this lower CO2 extreme of 25μatm. By Figure 5 it looks like G. oceanica outcompetes E hux at temps > 25C at 25μatm CO2.

Changed to “At extreme CO2 levels of 25 and 4000 μatm G. oceanica is only projected to reach higher growth rates than E. huxleyi at temperatures above 25.5 and 29oC, respectively (Figure 5).”

-Page 14, lines 1-3: This is a major finding of this study and should be put in the abstract.

It is already mentioned on line 6. Nevertheless, we could add “However, the greater sensitivity of G. oceanica to increasing [CO2] is partially mitigated by increasing temperatures.”

-Page 14, line 4/5: The sentence seems like it shouldn’t have the “under a broader range of CO2 conditions” part at the end. Under higher temperature alone (holding CO2 at about 400μatm) G. oceanica outcompetes E hux at temps > 22C. Or perhaps I’m misunderstanding this sentence completely?

Yes, this is a misunderstanding. What we mean by this is that as temperatures alone increase, the range of CO2 conditions under which G. oceanica outcompetes E. huxleyi becomes broader (i.e. expands from 300-500μatm to 200-600μatm). We will make this more clear within the section with the following change “Under increasing temperatures, but constant CO_2 levels, the range of CO_2 conditions under which G. oceanica outcompetes E. huxleyi expands (e.g. from ~100-600μatm at 24oC to ~250-1100μatm at 26oC)".

-Page 14, last paragraph of section 4.4.2: This would be better in a "Limitations of this study" section, as mentioned above.

See reply for the Page 12, line 12 comment.

-Page 15, line 12: By "productivity", do you mean calcification?

It is production of particulate inorganic carbon. This will be clarified.

-Page 15, lines 14-22: Would this paragraph better fit in the Results section?

We have opted to leave it where it is as it is part of the general discussion on how well our CCPP estimates fit to satellite derived CCPP.

-Page 16, lines 8-20: Could it be that E huxleyi CCPP just matches better because it's so much more abundant than G. oceanica?

While that would help, abundance alone does not completely control global PIC production. It is also the ratio of abundance/ growth to PIC production. The thought was that adding G. oceanica might help improve the fit by accounting for the greater amount of PIC production made by more heavily calcifying species in warmer regions.

-Page 16, line 14/15: I do not understand this sentence. So the combined CCPP in the North Pacific and Atlantic is greater or less than the E huxleyi CCPP?

Yes, as mentioned at the end of the sentence, all differences are relative to the E. huxleyi alone fit.

-Tables: -Tables 2 and 3: Put parentheses around units for $K_{1/2}CO_2inhib$ and $K_{1/2}CO_2sat$ in tables.

We will adopt this suggestion.

-Figures: -Figures 1 and 2: Indicate that this data is just for E. huxleyi in the caption. Also, show relevant CO2 range with a shaded area as in Sett et al., 2014 and indicate average oceanic CO2 concentration at present day.

We will adopt the first suggestion. As for the second, we will add a range of current day oceanic CO2 concentrations. Based on the carbonate chemistry data used for our global projections, modern CO2 concentrations range from 8.45-29.94 μmol kg-1. We shall add these boundaries as a shaded area in figures 1 and 2.

-Figure 3: Each "slice" looks the same.. maybe there's a better way to show differences between light levels or lack thereof? Also I do not understand the colors – add color legend.

Figure 3 is a full three dimensional niche comparison between E. huxleyi and G. oceanica. The visual similarity of slices at different light levels shows an important point, i.e. a small influence of light in modulating the CO2 and temperature response. A figure legend will be added.

-Figure 4: Make the μEH >μGO bigger or put it next to the color bar. It's a bit hard to notice and this is critical for understanding the figure.

We will make the font bigger.

-Figure 5: same suggestion as for Figure 4.

We shall adopt the requested changes.

-Figure 7: It needs to be mentioned in the caption that these maps are CCPP for Ehuxleyi only.

We will adopt the suggestion.

-Figure 8: Again, this is just CCPP for E huxleyi, right? This should be indicated in the figure caption. Also, a little map of the provinces (like in the supplemental section) would be great next to these bar plots. Having a map next to this data would make the figure much more relatable.

Yes it is, and this will be made clearer. We have moved the map into the same figure as the bar plots.

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