

A.J. Poulton (Referee) • Comment 1. Is strain PML B92/11 (isolated from Bergen, Norway) the best strain of *E. huxleyi* to present a niche description of *E. huxleyi*? My query here is whether the authors have considered the potential need to consider multiple strains when trying to describe the fundamental and realised niche of the species *E. huxleyi*. Though the authors state that cold-water (Southern Ocean) strains need to be considered more, would not a broader study of several strains of *E. huxleyi*, isolated from various geographical regions, result in a better description of the species as a whole? Related to this is whether the authors have considered examining different (geographically) strains of *G. oceanica* and whether the limitations of *G. oceanica*'s niche could relate to the limited number of strains available for this species? These comments are not meant to detract from the present study, but rather emphasize the broader context.

We agree that considering multiple strains, from diverse ocean regions, would benefit our study in describing the fundamental and realised niches for a species in more general terms. Nevertheless, despite the fact that our realised niche projections are based on only one strain for each species, they do generally fit to modern day observations. This indicates that the differences in requirements and sensitivities of the two species as described here are large enough to be revealed by choosing only two representatives. This has now been detailed in the final paragraph of section 4.4.2 (page 14 lines 31-33 and page 15 lines 1-3) as follows “Considering multiple strains, from diverse ocean regions, would aid our study in describing the fundamental and realised niches for a species in more general terms. However, even though our realised niche projections are based on only one strain for each species, they do generally agree with experimental observations of other strains, and with planktonic and sediment observations of each species as a whole. This indicates that the differences in requirements and sensitivities of the two species as described here are large enough to be revealed by choosing only one representative for each species.”

• Comment 2. The authors use a ‘recently proposed metric’ for coccolithophore calcification rates (CCPP), but proposed by who? No reference is mentioned in the paper. Could the authors provide more context and information on this new metric? This metric was proposed by us in a recently published paper. We have added the reference for this metric on page 3 line 14.

Specific points • Pg 1, Ln 4 (Ln 29) – *Emiliania huxleyi* is certainly one of the most abundant species, but not sure if *G. oceanica* can be classified in the same category. The two are common, though *E. huxleyi* has such a broad bio-geographical range compared to a narrower one for *G. oceanica* and generally a tropical range. Maybe relative abundance is not the characteristic to emphasize and either a commonality in many coccolithophore communities or bloom-formation by the two is more relevant (to global PIC production).

We agree and have changed the wording on page 1 lines 4-5 to: “the two most common bloom-forming species in present day coccolithophore communities appear adapted to. . .”

• Pg 1, Ln 13 – As well as the R^2 of the correlation, it would be good to know what the slope of the line looks like and the p-value in the abstract.

We have added the p-value and slopes to the abstract and discuss the slope of the line on page 16 lines 10-20.

• Pg 8, Ln 13-15 – Have the authors considered how total cell carbon (PIC+POC) to PON ratios would influence their data? In many ways, the N requirement of a coccolithophore cell is to produce both the PIC and POC. Also, are the PIC:POC ratios of 1 and 2 for *E. huxleyi* and *G. oceanica*, respectively, averages of the values given on Lines 23-24? Some justification for the use of these values, given the ranges known in the literature, is needed.

We have justified/explained total cell carbon:PON and the PIC:POC values as follows. “We first assumed a Redfieldian ratio of 106:16 C:N to determine the maximum POC production possible from the amount of available nitrate. We then calculated the amount of PIC which would be co-produced based on a mean PIC:POC. The average PIC:POC of *E. huxleyi* and *G. oceanica* was calculated as the average of all treatments between 300-1000 μatm from Sett et al. (2014), Zhang et al. (2015) and this study. Based on these averages (PIC:POC of 0.8 and 1.35 for *E. huxleyi* and *G. oceanica*, respectively), and assuming Redfieldian production a corresponding PIC:PON of 5.3 and 8.94 was calculated.” This explanation has now been included on page 8 (lines 31-33) and 9 (lines 1-3).

• Pg 14, Lns 21-23 – Surprised the review article by Monteiro et al. (2016) is not mentioned when considering viral attack and top-down effects as this article concluded that these were key considerations in the ecology of coccolithophores.

We have added a reference to the review article on page 15 lines 16-17. • Pg 16, Lns 2 and 3 – Rather than citing the PhD thesis of Charalampopoulou (2011), why don't the authors cite the peer-reviewed papers derived from this piece of work that address these points? Charalampopoulou et al. (2011) Irradiance and pH affect coccolithophore community composition on a transect between the North Sea and the Arctic Ocean. Marine Ecology Progress Series 431, 25-43, doi: 10.3354/meps09140. Charalampopoulou et al. (2016) Environmental drivers of coccolithophore abundance and calcification across Drake Passage

(Southern Ocean). Biogeosciences 13, 5917-5935, doi: 10.5194/bg-13-5917-2016.

We have adopted the reviewer's suggestion on page 16 lines 34 and 35.

• Pg 16, Ln 23 – Consider the use of the term ‘benefit’ in terms of *E. huxleyi* outcompeting *G. oceanica*.

Instead we have stated on page 17 line 20 “*E. huxleyi* will gain further competitive advantage over *G. oceanica*.”

- 5 • Pg 16, Ln 27 – What are coccolithophore dominated ecosystems? Please phrase in a more specific way (e.g. where coccolithophores are abundant enough to potentially influence the air-sea CO₂ flux (e.g. coccolithophore blooms) or dominate the deep-sea flux of particulate material (e.g. subtropical gyres). Coccolithophores never dominate ecosystems.

We have changed this on page 17 lines 22-25 to: “Such changes could have significant implications for climate feedback mechanisms, one being the relative strengths of the organic and inorganic carbon pumps in ecosystems where coccolithophores are abundant enough to significantly impact the air-sea CO₂ flux (e.g. coccolithophore blooms) and/or dominate the deep-sea flux of particulate material (e.g. subtropical gyres).”

10 Figures. • Fig 3 - Missing legend that is on Fig 4, consider swapping figures around or reproducing the legend.

A legend has been added to Figure 3.

- Fig 6 – This appears to be a rather unconvincing relationship. Is it possible to plot the 95% CI limits for the relationship? In addition, is there a sampling depth issue here that results in greater amount of data at high temperatures? That is to say, is the distribution of data related to more shallow tropical sediment samples than deep cold sub-polar sediment samples?

We have added 95% prediction bounds based on new observations for the global relationship. The fact that only the Atlantic basin does not entirely follow the trend has been mentioned in the text of the paper in more detail now. On page 14 lines 17-20 we have stated the following: “It is noted, however, that samples from the south-equatorial to equatorial Atlantic Ocean in Boeckel et al. (2006) do not follow the general temperature trend observed in other ocean basins (Figure 6). In this location it appears that *G. oceanica* abundance is driven more by increasing nutrient concentrations than by temperature. It seems oceanic upwelling in this region is driving a different relationship between *E. huxleyi* and *G. oceanica* than observed in other areas.” There is very little sediment sampling data at high latitudes in general let alone which contains these species. There is a disproportionately large amount of sampling in the warmer tropical areas. Also, we selected only samples which were above the lysocline and therefore were not affected by the possible confounding effects of differential dissolution of coccoliths.

- 25 • Fig 8 – Would it be more appropriate to plot as scatter plots where each data point is from each province? Maybe this would emphasize better how well the two agree and in which provinces they do not agree?

While using a scatterplot does emphasise that the two do not agree in some provinces, it also makes it more difficult to determine which provinces do and do not agree. For the purpose of clearly comparing each province in each season quickly, and having now included more details and a discussion on the slope of the fits, we feel that the barplot works best.

Anonymous (Referee 2) 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 at the beginning of Abstract describing why these two particular species are being compared would be helpful.

1. We have modified page 1 lines 9-10 to “For a future RCP 8.5 climate change scenario (1000 μatm fCO₂) we project a CO₂ driven niche contraction for *G. oceanica* to regions of even higher temperatures.” 2. We have modified page 1 lines 13-16 to “Based on *E. huxleyi* alone, as there was interestingly a better correlation than when in combination with *G. oceanica*, and excluding the Antarctic province from the analysis we found a good correlation between CCPP and satellite derived PIC in the other regions 15 with an R² of 0.73, p<0.01 and a slope of 1.03 for Austral winter/Boreal summer and an R² of 0.85, p<0.01 and a slope of 0.32 for Austral summer/Boreal winter.” 3. We have modified lines 4-5 of the abstract to “Based on our analysis, the two most common bloom-forming species in present day coccolithophore communities appear to be.”

45 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? How could this affect CaCO₃ production and growth rate in coccolithophores? How could increasing CO₂ affect growth rate/ calcification of coccolithophores? 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 have modified the text on page 2 lines 4-11 to “Under current scenarios, ocean temperatures are projected to increase from 2.6 to 4.8°C 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 and Salvucci, 2000; Zondervan et al., 2002; Helm et al., 2007; Pörtner and Farrell, 2008). Meanwhile, reduced nutrient availability could diminish overall productivity.”

• Page 2 line 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. oceanica* tend to thrive? Also mention that there are several different morphotypes 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 have added the following text in page 2 line 15 “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 been 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 several 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; Andrulleit 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. oceanica* niche comparison.

We have added the following to the end of the paragraph on page 3 lines 5-14 “Finally, we compare satellite derived particulate inorganic carbon estimates with a recently proposed metric for coccolithophore success on the community level, i.e. the temperature, light and carbonate chemistry speciation dependent calcium carbonate potential (Gafar et al. 2018).”

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 985atm (about 50mol kg⁻¹ aqueous CO₂), corresponds to a 4.8°C temperature increase, then why go up to 250mol 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 have made our rationale more clear in the methods section by adding the following to page 3 line 17: “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 are required. Hence, 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 have added the requested information to page 3 line 19.

• 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.

We have added the following information to page 5 lines 4-8. “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 con-

ditions due to enhanced air/water CO₂ gas exchange during regular cell abundance monitoring. As a result, at some extreme CO₂ levels there was an initial lag phase and therefore growth rates were calculated from densities only during the exponential part of the growth phase.”

- 5 • 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 multi-variate 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.

- 15 • 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”
- 20 We have rewritten the sentence as suggested above on page 7 lines 21-22.

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

The citation for the CCPP metric is now referenced on page 7 line 32.

• Page 8, line 14: Need citation for the PIC:POC ratios used for *E. huxleyi* and *G. oceanica*

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

- 25 • 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. oceanica* 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 have now stated on page 9 lines 19-20 “While three CCPP scenarios are presented above, only the results with the highest correlation to satellite PIC is shown and discussed below.”

- 30 • Page 8, lines 26 and 27: Need parentheses around year for citations Gregg and Casey (2007) and Longhurst (2007). We have adopted this suggestion on page 9 lines 14 and 15.

- 35 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 have adopted this suggestion by changing headings for sections 3.1, 3.2 and 3.3 to “*E. huxleyi* responses to ...”.

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

- 40 We have changed the sentence at the start of section 3 (page 9 lines 22-23) 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 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$) and temperature (10-20°C) 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.

- 45 We have changed the sentence at the start of section 3.1 (page 9 line 26) to “Based on fits of Eq. (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 K1/2 sat range from 0.85 to almost 5 mol 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 CO₂ concentration, between the three processes, required to support half of maximum rates is less than 1-2 μmol kg⁻¹. We have clarified this by changing this sentence (page 9 lines 27-29) to “Growth, calcification and photosynthetic carbon fixation rates required similar CO₂ concentrations, with differences of less than 3 μmol kg⁻¹ under comparable temperature and light conditions, to stimulate rates to half the maximum, K1/2CO₂sat (Table 2, Table 3).”.
- Page 9, lines 8-10: Mention what are the optimal CO₂ concentrations and put this into units of atm 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 K1/2 inhib reached? More specifics would give the reader more useful information.
- We have added the CO₂ concentrations for optima and K1/2 inhib on page 9 lines 30-31 and page 10 lines 1-2. 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”
- We have changed these sentences (page 10 lines 6-8) to “CO₂ half saturation concentrations (K1/2CO₂sat) 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 (K1/2CO₂inhib) 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. oceanica* data would be helpful. This could be done through line plots comparing the metabolic rates of the two species under varying CO₂ 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 CO₂ under different light conditions is already presented for easy comparison in a supplementary table. We have added this cross-reference to page 11 line 9. 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 CO₂ 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 CO₂ optima of 11 mol kg⁻¹ is not that small.
- We have changed this (page 11 lines 19-21) to “Changes in temperature produced little (<1 μmolkg⁻¹) change in CO₂ substrate half-saturation (K1/2CO₂sat) levels, at least within the measured range (Figure 1, Table 2). CO₂ requirements for optimum rates tended to slightly decrease with warming temperatures. Similar results were observed for.....”
- Page 11, line 5: Unneeded commas around “at least some”
- Commas on page 11 line 29 have been removed.
- 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.
- 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 5000atm CO₂? Please see our response to the comment on Page 3 line 4.
 - 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. huxleyi* 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 CO₂ 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”
- The word figure has been capitalised (page 13 line 13).
- Page 13, line 7: I think it’s well established that *E. huxleyi* is a generalist, given its widespread distribution from subpolar to tropics.
- We have changed this (page 13 lines 30-31) to “For example, *E. huxleyi* is projected to reach higher growth rates than *G. oceanica* under a broader range of temperature, light and CO₂ conditions (Figures 3, 4 and 5), supporting the notion that *E. huxleyi* is rather a generalist.”
- Page 13, line 9: Unneeded comma after “niche”
- Comma on page 14 line 1 has been removed.
- Page 13, line 25: Reference needed for this *E. huxleyi* warm water strain that outcompete *G. oceanica* at temps > 25°C
- This observation is based on the data compiled in Figure 6. The data sources have been referenced in the figure caption. We have also re-worded the sentence on page 14 lines 20-21 to read “Globally the data suggests that dominance switches from *E. huxleyi* to *G. oceanica* at temperatures above 25°C which is similar to our projections.”
- 20 • Page 13, line 32/33: I’m confused by this lower CO₂ extreme of 25 atm. By Figure 5 it looks like *G. oceanica* outcompetes *E. hux* at temps > 25°C at 25 atm CO₂.
- For clarity we have changed this section (page 14 lines 25-30) to read “CO₂ level also influences the relative growth rates of *E. huxleyi* and *G. oceanica*. Under current day levels of 400 µatm, *E. huxleyi* would dominate at temperatures up to 22°C (Figure 5). However, at higher and lower CO₂ levels, *E. huxleyi* begins to outgrow *G. oceanica* at progressively higher temperatures.
- 25 At the same time, combined warming in a future ocean would partially mitigate the higher CO₂ sensitivity of *G. oceanica* (Figure 5). Nevertheless, over the naturally observed temperature range, *G. oceanica*’s niche would be expected to decrease towards higher CO₂ levels.”
- 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 have added “However, the greater sensitivity of *G. oceanica* to increasing [CO₂] is partially mitigated by increasing temperatures.”
- 30 • 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 400 atm) *G. oceanica* outcompetes *E. hux* at temps > 22°C. 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 300-500atm to 200-600atm). More importantly *G. oceanica* becomes less sensitive to high CO₂ conditions under elevated temperatures which is the point we wanted to highlight. We have made this more clear on page 14 lines 28-30 with the following change “At the same time, combined warming in a future ocean would partially mitigate the higher CO₂ sensitivity of *G. oceanica* (Figure 5). Nevertheless, over the naturally observed temperature range, *G. oceanica*’s niche would be expected to decrease towards higher CO₂ levels.”
- 40 • 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 (PIC). This has been clarified by changing the sentence to “The fact that three other global estimates, based on different sets of environmental parameters, all estimate very little PIC productivity in the Southern Ocean seems to support this theory.” On page 16 lines 5-6.
- 45 • Page 15, lines 14-22: Would this paragraph better fit in the Results section?
- We have opted to leave it where it is (page 16 lines 10-19) 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. ocean-*

ica?

- 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 (Now on page 17 lines 5-17).
- 5 • 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 (Now on page 17 lines 11-12). Tables: • Tables 2 and 3: Put parentheses around units for $K1/2CO_2$ inhib and $K1/2CO_2$ sat in tables.
- 10 We have adopted this suggestion.
- Figures: • Figures 1 and 2: Indicate that this data is just for *E. huxleyi* in the caption. Also, show relevant CO_2 range with a shaded area as in Sett et al., 2014 and indicate average oceanic CO_2 concentration at present day.
- We have adopted the first suggestion by now stating “(A) Fitted particulate inorganic carbon (PIC), (B) particulate organic carbon (POC) production, and (C) growth rates (solid lines) of *E. huxleyi* in response. . . .” in the caption. As for the second,
- 15 based on the carbonate chemistry data used for our global projections, modern CO_2 concentrations range from 8.45-29.94 $\mu mol\ kg^{-1}$. We have added 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 CO_2 and temperature response. A figure legend has now been added.
- 20 • Figure 4: Make the EH >GO 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 have increased the font size.
- 25 • Figure 5: same suggestion as for Figure 4.
- We have adopted the requested changes.
- Figure 7: It needs to be mentioned in the caption that these maps are CCPP for *E. huxleyi* only.
- The caption has been amended to “Austral summer/Boreal winter (A) and Austral winter/Boreal summer (D) satellite measured particulate inorganic carbon. Austral summer/Boreal winter (B) and Austral winter/Boreal summer (E) *E. huxleyi* based CCPP estimates accounting for carbonate chemistry (substrate and hydrogen ion concentrations), light intensity and temperature.”.
- 5 • 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.
- 10 Yes, it is. We have moved the map into the same figure as the bar plots and changed the caption to “Satellite derived particulate inorganic carbon (black bars) and *E. huxleyi* based CCPP (white bars) estimates for major ocean biogeographical provinces as percentages of total production in (A) Austral winter/Boreal summer and (B) Austral summer/Boreal winter. (C) Major ocean biogeographical province definitions.”.
- 15 Community comments Mario Cachao • You present a very interesting and useful piece of work. You selected the two species you refer as the most common. *Emiliania huxleyi* (Eh) is unquestionably the currently dominating species in oceanic niches. *Gephyrocapsa oceanica* (Go) is for sure the most abundant but in neritic domain (at least in my area, not sure about Australia), not exactly the most common in the overall oceans. In addition, from a paleoecological point of view, records of Eh are always compared to another small placolith species (small Gephyrocapsids; sG), not to Go, both in terms of relative and absolute
- 20 abundances. I understand that Eh and Go are among those coccolithophores that better perform in cultures but shouldn’t we compare Eh against sG instead? What’s your opinion?
- It is more that these two species are the most common in terms of their presence in coccolithophore communities rather than their dominance. Both species have a broad distribution across multiple ocean basins, for detail please see our response to reviewer 2 Page 2 line 18. It is this reason, plus the fact that data on responses to changing CO_2 , temperature and light are
- 25 available for both species, that we decided to compare the two species.

It would also be of interest to compare *E. huxleyi* against the small Gephyrocapsids. However, from what we understand the small Gephyrocapsids consist of multiple small Gephyrocapsa spp. which are not always identified to the species level (e.g. Table 3 Flores et al. 1999). As such, a niche comparison with *E. huxleyi* would be very difficult to accomplish from an experimental point of view.

- 30 *G. oceanica* is often mentioned alongside *E. huxleyi* in sediment core data (i.e. McIntyre and Be 1967, Chen and Shieh 1982, Roth and Coulburn 1982, Knappertsbusch et al. 1993, Findlay and Flores 2000, Andruleit and Rogalla 2002, Boeckel et al. 2006, Fernando et al. 2007, Saaveda-Pellitero et al. 2010). Further, it seems that in longer geological records that *E. huxleyi* is usually compared to larger Gephyrocapsa species such as *G. mullerae*, *G. caribbeanica* and *G. oceanica* as well as the small Gephyrocapsids (Flores et al. 1997, Findlay and Florin 2000, Flores et al. 2003, Backman et al. 2009). So, we believe it is
- 35 equally reasonable to compare *E. huxleyi* and *G. oceanica* as it is to compare *E. huxleyi* to the small Gephyrocapsids.

A three-dimensional niche comparison of *Emiliana huxleyi* and *Gephyrocapsa oceanica*: Reconciling observations with projections

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Abstract. Coccolithophore responses to changes in carbonate chemistry speciation such as CO₂ and H⁺ are highly modulated by light intensity and temperature. Here we fit an analytical equation, accounting for simultaneous changes in carbonate chemistry speciation, light and temperature, to published and original data for *Emiliana huxleyi*, and compare the projections with those for *Gephyrocapsa oceanica*. Based on our analysis, the two most **common bloom-forming species in present day**
5 **coccolithophore communities appear to** be adapted for a similar fundamental light niche but slightly different ones for temperature and CO₂, with *E. huxleyi* having a tolerance to lower temperatures and higher CO₂ levels than *G. oceanica*. Based on growth rates, a dominance of *E. huxleyi* over *G. oceanica* is projected below temperatures of 22°C at current atmospheric CO₂ levels. This is similar to a global surface sediment compilation of *E. huxleyi* and *G. oceanica* coccolith abundances suggesting temperature dependent dominance shifts. For a future RCP 8.5 climate change scenario (1000 μatm fCO₂) we project a **CO₂**
10 **driven niche contraction for *G. oceanica* to regions of even higher temperatures. However, the greater sensitivity of *G. oceanica* to increasing CO₂ is partially mitigated by increasing temperatures.** Finally, we compare satellite derived particulate inorganic carbon estimates in the surface ocean with a recently proposed metric for potential coccolithophore success on the community level i.e. the temperature, light and carbonate chemistry dependent CaCO₃ production potential (CCPP). **Based on *E. huxleyi* alone, as there was interestingly a better correlation than when in combination with *G. oceanica*, and excluding the Antarctic**
15 **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, p<0.01 and a slope of 1.03 for Austral winter/Boreal summer and an R² of 0.85, p<0.01 and a slope of 0.32 for Austral summer/Boreal winter.

1 Introduction

20 Since the Industrial Revolution in the late 18th century, burning of fossil fuels, as well as wide scale deforestation have contributed to significant increases in atmospheric carbon dioxide, CO₂ (IPCC, 2013a). Depending upon the decisions in the next few decades, atmospheric CO₂ levels are projected to reach between 420 μatm (RCP2.6 scenario) and 985 μatm (RCP8.5 scenario) by 2100 (Caldeira and Wickett, 2005; Orr et al., 2005; IPCC, 2013a). To date approximately one third of the anthropogenic carbon emissions have been absorbed by the world's oceans (Sabine et al., 2004). As atmospheric partial pressures of CO₂ (pCO₂) increase, CO₂ concentrations in the surface ocean also increase, resulting in increased bicarbonate and hydrogen

25 ions but also in decreased carbonate ion concentrations and pH (Doney et al., 2009; Schulz et al., 2009). These changes, often termed ocean carbonation and acidification, can have both positive and negative effects for different phytoplankton species and groups (e.g. Engel et al. 2005; Feng et al. 2010; Moheimani and Borowitzka 2011; Endo et al. 2013; Schulz et al. 2017).

Associated with rising $p\text{CO}_2$ is the phenomenon of global warming. Under current scenarios, ocean temperatures are projected to increase from 2.6 to 4.8°C 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 and Salvucci, 2000; Zondervan et al., 2002; Helm et al., 2007; Pörtner and Farrell, 2008). Meanwhile, reduced nutrient availability could diminish overall productivity.

Coccolithophores play an important role in the marine carbon cycle through the precipitation of calcium carbonate, via calcification and the formation and settling of coccolith aggregates, as well as inorganic carbon fixation by photosynthesis (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 having been 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 and Bé, 1967; Winter et al., 1994; Hagino and Okada, 2006; Boeckel and 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 several 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 Bé, 1967; Okada and Honjo, 1975; Roth and Coulbourn, 1982; Knappertsbusch, 1993; Eynaud et al., 1999; Andruleit et al., 2003; Saavedra-Pellitero et al., 2014), however with a tendency towards warmer waters with very few specimens observed below 13°C (McIntyre and Bé, 1967; Eynaud et al., 1999; Hagino et al., 2005). It is well established that rising $p\text{CO}_2$ will have significant effects on coccolithophorid growth, calcification and photosynthetic carbon fixation rates (Riebesell et al., 2000; Bach et al., 2011; Raven and Crawford, 2012). Furthermore, it has been shown that the response to rising $p\text{CO}_2$ of both *G. oceanica* and *E. huxleyi* is strongly influenced by light intensity and temperature (Zondervan et al., 2002; Schneider, 2004; De Bodt et al., 2010; Sett et al., 2014; Zhang et al., 2015). However, to which degree species specific responses may shape individual distribution and abundance in the future ocean is far less clear.

This is because the distribution and abundance of a species is controlled by several factors. Firstly, each species has a specific range of environmental conditions under which they can successfully grow and reproduce called the fundamental niche. The fundamental niche describes the multi-dimensional combination of environmental conditions, such as temperature, light and $p\text{CO}_2$, required for survival of a species assuming no other species are present (Leibold, 1995). However, species do not exist

in a vacuum and where the niche of a species overlaps with another species interactions such as competition for resources and predation can occur (Hutchinson, 1957; Leibold, 1995), resulting in the realised niche (Leibold, 1995; Zurell et al., 2016). Hence it is not only important to determine how environmental change shapes the fundamental niche of individual species, but also consider the impact of niche overlap of different species in shaping the realised niches and hence community composition.

In the present study, we therefore compare species specific sensitivities and responses to combined light, temperature and carbonate chemistry changes of two of the most abundant coccolithophores *Emiliania huxleyi* and *Gephyrocapsa oceanica*. For that purpose, *E. huxleyi* was grown at twelve $p\text{CO}_2$ levels and five light intensities and growth, photosynthetic carbon fixation and calcification rates were measured in response. These data were then combined with a previously published data set on temperature and CO_2 interaction (Sett et al., 2014) and fitted to an analytical equation describing the combined effects of changing carbonate chemistry speciation, light and temperature. The resulting projections are then compared to those previously published for *G. oceanica* (Gafar et al., 2018) in an attempt to assess their individual success and potential realised niche in a changing ocean. **Finally, we compare satellite derived particulate inorganic carbon estimates with a recently proposed metric for coccolithophore success on the community level, i.e. the temperature, light and carbonate chemistry speciation dependent calcium carbonate potential (Gafar et al., 2018).**

2 Methods

2.1 Experimental set-up

To accurately identify optimal conditions, tipping points and sensitivities of rates in response to changing CO_2 , light and temperature, a broad range of experimental conditions are required. Hence, mono-specific cultures of the coccolithophore *E. huxleyi* (strain PML B92/11 morphotype A isolated from Bergen, Norway) were grown in artificial seawater (ASW) at 20°C and a salinity of 35 across a $p\text{CO}_2$ (partial pressure of CO_2) gradient from $\sim 25\text{-}7000 \mu\text{atm}$. Light intensities were set to 50, 400 and $600 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ of photosynthetically active radiation (PAR) on a 16:8 h light-dark cycle in a Panasonic Versatile Environmental Test Chamber (MLR-352-PE). An additional set of cultures was also incubated at $1200 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ under a Philips SON-T HPS 600W light in a water-bath set to 20°C . Light intensities at each bottle position for all experiments were measured using a LI-193 spherical sensor (LI-COR). Cells were pre-acclimated to experimental conditions for 8-12 generations. To account for differences in growth rate between the extreme high/low CO_2 treatments and the intermediate CO_2 treatments, initial cell densities chosen between $20\text{-}80 \text{ cells ml}^{-1}$. Treatments were run using a dilute-batch culture setup, mixed daily and harvested before dissolved inorganic carbon (DIC) consumption exceeded 10%.

2.2 Media

Artificial seawater (ASW) with a salinity of 35 was prepared according to Kester et al. (1967). ASW was enriched with f/8 trace metals (EDTA bound Fe, Cu, Mo, Zn, Co, Mn) and vitamins (thiamine, biotin, cyanocobalamin) according to Guillard

(1975), $64 \mu\text{mol kg}^{-1}$ nitrate (NO_3^-), $4 \mu\text{mol kg}^{-1}$ phosphate (PO_4^{3-}), 10 nmol kg^{-1} SeO_2 and 1 ml kg^{-1} of coastal seawater (collected at Shelly beach, Ballina, NSW, Australia) to prevent possible limitation by trace elements during culturing which had not been added to the artificial seawater mix. ASW medium was sterile-filtered ($0.2 \mu\text{m}$ pore size, WhatmanTM Polycap
5 75 AS) directly into autoclaved acclimation (0.5 L) or experimental (2 L) polycarbonate bottles (Nalgene[®]), leaving a small head-space for the adjustment of carbonate chemistry conditions.

2.3 Carbonate chemistry manipulation, measurements and calculation

Carbonate chemistry, i.e. total alkalinity (TA) and dissolved inorganic carbon (DIC), for each treatment was adjusted through calculated additions of hydrochloric acid (certified 3.571 mol L^{-1} HCl, Merck) and Na_2CO_3 (Sigma-Aldrich, TraceSELECT[®]
10 quality, dried for 2 hours at 240°C). Samples for TA and DIC measurements were taken at the end of the experiment. TA samples were filtered through GF/F filters, stored in the dark at 4°C and processed within 7 days (Dickson et al. 2007 SOP 1). TA samples were measured by potentiometric titration using a Metrohm Titrino Plus automatic titrator with 0.05 mol kg^{-1} HCl as the titrant, adjusted to an ionic strength of 0.72 mol kg^{-1} with NaCl (Dickson et al. 2007 SOP 3b).

15 DIC samples were sterile filtered by gentle pressure filtration with a peristaltic pump ($0.2 \mu\text{m}$ pore size polycarbonate, Sartorius) into glass stoppered 100 ml bottles (Schott Duran) with overflow of at least 50% of bottle volume similar to Bockmon and Dickson (2014), sealed without head-space and stored in the dark at 4°C until processing within 7 days. To determine DIC, 2 ml of sample was analysed on a Marianda AIRICA system by acidification with 10% phosphoric acid to convert all DIC into CO_2 , followed by extraction with N_2 (5.0) and concomitant CO_2 analysis with an IR detector (LI-COR LI-7000 $\text{CO}_2/\text{H}_2\text{O}$
20 analyser). Both TA and DIC measurements were calibrated against Certified Reference Materials (batches 139, 141, 150) following Dickson (2010). Initial DIC and TA concentrations were estimated by adding measured total particulate carbon build-up during incubations to measured final DIC, and double the particulate inorganic carbon build-up during incubations to measured final TA concentrations. Carbonate chemistry speciation for each treatment was calculated from mean TA, mean DIC, measured temperature, salinity and $[\text{PO}_4^{3-}]$ using the program CO2SYS (Lewis et al., 1998), the dissociation constants
25 for carbonic acid determined by Lueker et al. (2000), K_S for sulphuric acid determined by Dickson et al. (1990) and K_B for boric acid following Uppström (1974).

2.4 Particulate organic and inorganic carbon

Sampling started approximately two hours after the onset of the light period and lasted no longer than 3 hours. Duplicate samples for total and particulate organic carbon (TPC and POC) were filtered (-200 mbar) onto GF/F filters (Whatmann, pre-
30 combusted at 500°C for 4 hours) and stored in glass petri-dishes (pre-combusted at 500°C for 4 hours) at -20°C until analysis. POC filters were placed in a desiccator above fuming (37%) HCl for 2 hours to remove all particulate inorganic carbon (PIC). All filters were dried overnight at 60°C , and analysed for carbon content and corresponding isotopic signature according to Sharp (1974) on an elemental analyser (Flash EA, Thermo Fisher) coupled to an isotope ratio mass spectrometer (IRMS, Delta V plus, Thermo Fisher). Particulate inorganic carbon (PIC) was calculated by subtracting measured POC from TPC.

2.5 Growth

Cell densities were measured every 3-4 days after the commencement of the experiment using a flow cytometer (Becton Dickinson FACSCalibur) on high flow settings (58 $\mu\text{l}/\text{minute}$) for two minutes per measurement. Living cells were detected by their red autofluorescence in relation to their orange fluorescence in scatter plots (FL3 vs. FL2). **At both, the extreme low and high CO_2 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 CO_2 gas exchange during regular cell abundance monitoring. As a result, at some extreme CO_2 levels there was an initial lag phase and therefore growth rates were calculated from densities only during the exponential part of the growth phase. After disregarding lag phase measurements, the majority of treatments had only two to three data-points in the exponential phase. As a result, specific growth rates were calculated as:**

$$\mu = \frac{\ln(C_f) - \ln(C_0)}{d} \quad (1)$$

where C_f represents cell densities at time of sampling, C_0 represents cell densities at the beginning of the exponential growth phase, and d is the duration of the exponential phase in days. Calcification and photosynthetic rates were calculated by multiplying cellular PIC and POC quotas with respective growth rates.

2.6 Fitting procedure

Coccolithophore metabolic rate (MR) responses of growth, calcification and photosynthetic carbon fixation to combined changes in temperature, light and carbonate chemistry speciation can be described as follows (Gafar et al., 2018).

$$\text{MR}(T,I,S,H) = \frac{k_1 \text{SIT}}{k_2 \text{HT} + k_3 \text{SHT} + k_4 \text{I} + k_5 \text{SI} + \text{SIT} + k_6 \text{SHI}^2 \text{T}^2} \quad (2)$$

where, k_1 ($\text{pg C cell}^{-1} \text{ day}^{-1}$ or day^{-1}), k_2 ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$), k_3 ($\text{kg mol}^{-1} \mu\text{mol photons m}^{-2} \text{s}^{-1}$), k_4 ($\text{mol kg}^{-1} \text{ } ^\circ\text{C}$), k_5 ($^\circ\text{C}$), k_6 ($\text{kg mol}^{-1} \mu\text{mol photons}^{-1} \text{ m}^2 \text{s } ^\circ\text{C}^{-1}$) are fit coefficients, and $\text{MR}(T,I,S,H)$ is the metabolic rate of photosynthesis, calcification or growth dependent on temperature (T), light intensity (I), substrate ($S = [\text{CO}_2] + [\text{HCO}_3^-]$) and $[\text{H}^+]$ (H). Inputs to the equation consisted of calculated CO_2 , HCO_3^- and H^+ (H in total scale) concentrations, as well as measured metabolic rates, and light (I) and temperature (T) levels of all treatments (please see below for information on temperature and light transforms).

25

Data from this study (Tables S1, S2) and Sett et al. (2014) were fitted to Eq. (2) using the non-linear regression fit procedure `nlinfit` in MATLAB (the Mathworks). The reason only these studies were chosen, from the multitude of *E. huxleyi* datasets, is because 1) they use the same strain (PML B92/11), 2) they have the same nutrient conditions and 3) they use the same carbonate chemistry manipulation methods. Nevertheless, the two chosen studies provided light (six levels) and temperature (three levels) interactions over a broad carbonate chemistry speciation range. It is noted that in both studies the carbonate chemistry system

30

is coupled, meaning that a change in CO₂ results in a change in pH. This method reflects the changes in carbonate chemistry speciation due to ongoing ocean acidification (Bach et al., 2011, 2013). However, some studies have examined the effects of decoupled carbonate chemistry where CO₂ is changed at a constant pH. This approach is used to tease apart the independent effects of H⁺ and CO₂ on physiological responses (see Bach et al. 2013). While Eq. (2) can also be used to explain responses under decoupled carbonate chemistry conditions (see Gafar et al. 2018 for details), the fit obtained here is only valid for coupled CO₂/pH changes as no data from decoupled experiments (i.e. Bach et al. 2011) has been used. The reason for this being that

5 Bach et al. (2011) does not contain data of temperature, light and carbonate chemistry interactions.

2.7 Temperature and light transformations

To reduce skew and to better accommodate certain features (i.e. light and temperature inhibition and limitation) both temperature and light data were transformed. Light data was square root transformed with light (I) = $\sqrt{\text{PFD}}$, where PFD is the photon flux density ($\mu\text{mol photons m}^{-2}\text{s}^{-1}$) of an incubation. To accommodate for known temperature inhibition below 2°C and above 30°C (Rhodes et al., 1995; van Rijssel and Gieskes, 2002; Helm et al., 2007; Zhang et al., 2014) at a much narrower experimental range (10-20°C), the upper and lower limits for *E. huxleyi* growth were added into the equation with a general transform of $T = (T_t - 2) \times (30 - T_t)$, where T_t is the temperature of an incubation. To accurately express the onset of high temperature inhibition, the transform was further modified with a square root transform to give $T = (T_t - 2) \times \sqrt{(30 - T_t)}$. This transform produces reasonable results when compared to the Eppley temperature envelope curve and the Norberg model

15 (see Gafar et al. 2018).

2.8 Physiological rate response parameter estimations to changes in carbonate chemistry, temperature and light

Equation (2) was used to assess the combined effects of carbonate chemistry, temperature and light on growth, calcification and photosynthetic carbon fixation rates, with a focus on general physiological features, such as limitation and inhibition, as well as how much variability could be explained. For growth, photosynthetic carbon fixation and calcification rates optimum CO₂ concentrations for maximum production rates (V_{max}) and half saturation values were calculated at each experimental light and temperature level. $K_{\frac{1}{2}}$ values consisted of: $K_{\frac{1}{2}\text{CO}_2^{\text{sat}}}$ which is the CO₂ concentration (at certain T and I) at which rates are saturated to half the maximum, and $K_{\frac{1}{2}\text{CO}_2^{\text{inhib}}}$, which is the CO₂ concentration (at certain T and I) at which high proton concentrations reduce physiological rates to half the maximum. Fitting results (R^2 , fit coefficients, p-values, F-values and degrees of freedom), as well as V_{max} , $K_{\frac{1}{2}}$ and CO₂ optima are presented in Tables 1, 2 and 3. Species specific differences in response to changing carbonate chemistry, temperature and light were assessed by comparing the above fit to that recently produced for *Gephyrocapsa oceanica* (Gafar et al., 2018).

25

2.9 Niche comparison

To examine the potential of ongoing ocean change to influence realised niches and hence individual success, ranges for light and temperature where both *Emiliania huxleyi* and *Gephyrocapsa oceanica* might be expected to co-exist were selected (i.e.

30 50-1000 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ and 8-30°C). *E. huxleyi* and *G. oceanica* were chosen for comparison as they are currently the only two species with response data over a range of carbonate chemistry, temperature and light conditions. Growth rates were selected as the point of comparison because they can be used as a measure of relative abundance and therefore dominance of a species, and because growth rates largely control carbon fixation rates. To assess competitive ability, and the potential realised niche, the difference in growth rates between the species was visualised using contour plots.

The effect of temperature on growth rates and hence potential dominance was then compared to phytoplankton community data from global surface sediment samples above the lysocline (McIntyre and Bé, 1967; Chen and Shieh, 1982; Roth and Coulbourn, 1982; Knappertsbusch, 1993; Andrulleit and Rogalla, 2002; Boeckel et al., 2006; Fernando et al., 2007; Saavedra-Pellitero et al., 2014). As *E. huxleyi* and *G. oceanica* have similar average numbers of coccoliths per cells, 28 and 21, respectively (Samtleben and Schroder, 1992; Knappertsbusch, 1993; Baumann et al., 2000; Boeckel and Baumann, 2008; Patil et al., 2014), the abundance ratio of *E. huxleyi* to *G. oceanica* coccoliths was here assumed to be a suitable proxy for species dominance. It is noted that *E. huxleyi* has been found to produce excess coccoliths towards the end of blooms when inorganic nutrients become limiting for cellular growth (Balch et al., 1992; Holligan et al., 1993; Paasche, 1998), which would result in an over-estimate of *E. huxleyi* dominance in our study. Nevertheless, given that the coccoliths ratio varies orders of magnitude in modern marine sediments, none of our general conclusions should be affected. Temperature for each sampling site was retrieved from the NOAA 1° resolution annual temperature climatology (Boyer et al., 2013).

15 **2.10 Global calcium carbonate production potential**

While our fit equation has previously explained variability in lab experiments quite well (Gafar et al., 2018), natural systems are much more complex, with the interactions of dozens of variables including temperature, light, nutrients, predation and competition all influencing productivity (Behrenfeld, 2014). As such we wanted to examine how **projections of productivity using our relatively simple equation** compared to coccolithophorid productivity patterns observed in natural systems. Productivity can be defined in a few ways, traditionally, changes in cellular calcification rates, in response to ocean change, have been used as indicator for the potential success of coccolithophores in the future ocean. However, the exponential nature of phytoplankton growth amplifies even small differences in cellular growth rates, when applied on the community level. For instance, a phytoplankton bloom occurring over one week at a growth rate of 1.0 d^{-1} and a starting cell density of 50 cells ml^{-1} would lead to a peak density of about $55,000 \text{ cells ml}^{-1}$. This is in stark contrast to conditions where growth is only 10% lower as peak cell densities, and hence biomass and PIC standing stock, will only be half.

Recently, a new metric was proposed, the CaCO_3 production potential (CCPP) which 1) should be a better representation of potential coccolithophore success on the community level and 2) can be tested against modern observations of surface ocean CaCO_3 distribution (Gafar et al., 2018). CCPP is defined as the amount of CaCO_3 produced within a week by a coccolithophore community (with a set starting cell count) for a certain environmental condition, calculated from Eq. (2) derived growth rates and inorganic carbon quotas. Inorganic carbon quotas are calculated as the quotient of calcification and growth

rates. As CCPP is calculated from calcification and growth rates, it accounts for the individual effects of temperature, light and carbonate chemistry on growth rates and on carbon production. It was for these reasons that CCPP was the metric chosen for comparison.

5

Provided values for temperature, light, substrate ($\text{CO}_2 + \text{HCO}_3^-$) and hydrogen ion concentrations (H) for the surface mixed layer, coccolithophore CaCO_3 production potential can be projected for the world oceans. CCPP can then be cautiously evaluated against and compared to satellite derived global particulate inorganic carbon concentration estimates (PIC_s). As inorganic nutrients are a critical factor influencing phytoplankton abundance, and especially bloom formation, in the ocean (Browning et al., 2017) nitrate concentrations were also included in the analysis (for details see below). As a result, climatological datasets consisted of, World Ocean Atlas 2013 v2 (WOA) nitrate concentrations at 1° resolution (Boyer et al., 2013); SeaWiFS mixed layer depth (MLD 2° resolution) from de Boyer Montégut et al. (2004); surface photosynthetically available radiation (PAR $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ 9 km resolution) from the Moderate Resolution Imaging Spectroradiometer (MODIS)-Aqua (NASA Goddard Space Flight Center, 2014b); diffuse attenuation coefficients at 490nm (9 km resolution) from Pascal (2013); and NOAA dissolved inorganic carbon, $p\text{CO}_2$, pH (total scale), $[\text{CO}_3^{2-}]$, temperature and salinity ($4 \times 5^\circ$ resolution) from Takahashi et al. (2014). A 9 km resolution climatology for particulate inorganic carbon (PIC_s) concentration (mol PIC m^{-3}) was also retrieved from the Moderate Resolution Imaging Spectroradiometer (MODIS)-Aqua (NASA Goddard Space Flight Center, 2014a). Once acquired, all datasets were interpolated to a 1° resolution.

20 Hydrogen ion concentrations were calculated as $10^{-\text{pH}}$, CO_2 , after conversion of $p\text{CO}_2$ to $f\text{CO}_2$ as described in CO2SYS (Lewis et al., 1998), as $[f\text{CO}_2] * K_0$ (with K_0 being the temperature and salinity dependent Henry's constant), HCO_3^- as $[\text{HCO}_3^-] = \text{DIC} - ([\text{CO}_2] + [\text{CO}_3^{2-}])$, and substrate (S) as the sum of CO_2 and HCO_3^- concentrations. Mean mixed layer nitrate concentrations were calculated by determining concentrations for each depth and averaging from surface to the mixed layer depth for each grid cell. Mean mixed layer irradiance was calculated in one-meter depth increments for each grid cell as

$$25 \quad I = \sum_{i=1}^{\text{MLD}} = \exp^{-k_d(i)} * I_0 \quad (3)$$

where I is the average PAR ($\mu\text{mol photons m}^{-2}\text{s}^{-1}$), k_d is the attenuation coefficient (m^{-1}), MLD denotes the mixed layer depth in meters, and I_0 is the incident PAR at the surface ($\mu\text{mol photons m}^{-2}\text{s}^{-1}$).

30 Global coverage of oceanic nutrient concentrations are often limited to only a few macro-nutrients (nitrate, silicate, phosphate). However, concentrations of these nutrients are often strongly correlated (e.g. phosphate and nitrate in Boyer et al. 2013). To ensure there was sufficient nutrients to support the level of production estimated by CCPP, we opted to use a single nutrient, i.e. nitrate, in combination with a simple scaling metric. **We first assumed a Redfieldian ratio of 106:16 C:N to determine the maximum POC production possible from the amount of available nitrate. We then calculated the amount of PIC which would be co-produced based on a mean PIC:POC. The average PIC:POC of *E. huxleyi* and *G. oceanica* was calculated as the average**

5 of all treatments between 300-1000 μatm from Sett et al. (2014), Zhang et al. (2015) and this study. Based on these averages (PIC:POC of 0.8 and 1.35 for *E. huxleyi* and *G. oceanica*, respectively), and assuming Redfieldian production a corresponding PIC:PON of 5.3 and 8.94 was calculated. Hence, maximum CaCO_3 production potential (CCPP_{max}) in a grid cell would be 5.3 and 8.94 times the nitrate concentration for *E. huxleyi* and *G. oceanica* respectively. If estimated CCPP for a cell exceeded CCPP_{max} , and therefore the nitrate required to produce that much PIC, then it was replaced with the CCPP_{max} value. If CCPP
10 was less than C_{max} then no further changes were applied.

To ensure that mean global CCPP and mean global PIC_s would be of the same magnitude, starting cell counts for CCPP calculations were set at 1 ml^{-1} for *E. huxleyi* alone, 0.25 ml^{-1} for *G. oceanica* alone and 0.25 ml^{-1} for each species when combined. To allow comparison, CCPP and PIC_s were both converted to units of $\mu\text{mol PIC L}^{-1}$. All data were then averaged for Austral summer/Boreal winter (December-February) and Austral winter/Boreal summer (June-August). Austral summer/Boreal winter and Austral winter/Boreal summer were chosen as they provide prominent differences between minimum and maximum PIC, while spring and autumn do not. A direct comparison between PIC_s and CCPP was achieved by splitting results into major ocean biogeographical provinces following Gregg and Casey (2007) with the single change of adjusting the Antarctic and the north ocean regions to start at 45° as in Longhurst (2007) rather than 40° (Figure 8C). For each major
20 province, the total amount of PIC_s and CCPP for all comparable grid cells were calculated for Austral summer/Boreal winter and Austral winter/Boreal summer. For comparison, values for each basin and season were then converted into percentages of annual global (global summer plus global winter) PIC_s or CCPP production. Agreement between the satellite and CCPP estimates was then assessed using a linear correlation. While three CCPP scenarios are presented above, only the results with the highest correlation to satellite PIC is shown and discussed below.

25 3 Results

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 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$) and temperature (10-20°C) conditions (Table 1).

3.1 *E. huxleyi* responses to changing carbonate chemistry: CO_2 and H^+

30 Based on fits of Eq. (2), growth, calcification and photosynthetic carbon fixation rates all had a similar optimum curve response to the broad changes in carbonate chemistry speciation (Figure 1) regardless of temperature and light intensities. Growth, calcification and photosynthetic carbon fixation rates required similar CO_2 concentrations, with differences of less than 3 $\mu\text{mol kg}^{-1}$ under comparable temperature and light conditions, to stimulate rates to half the maximum, $K_{\frac{1}{2}\text{CO}_2\text{sat}}$ (Table 2, Table 3). Optimum CO_2 concentrations for calcification (8.4-19.1 $\mu\text{mol kg}^{-1}$) were slightly lower than for photosynthesis (9.9-52.1 $\mu\text{mol kg}^{-1}$) or growth (15-29.1 $\mu\text{mol kg}^{-1}$ Table 2, Table 3). At CO_2 concentrations beyond the optimum, a much higher

sensitivity to increasing $[H^+]$, i.e. $K_{\frac{1}{2}CO_2}^{inhib}$ was observed for calcification (47.4-118.5 $\mu\text{mol kg}^{-1}$) than for photosynthesis (73.0-250+ $\mu\text{mol kg}^{-1}$) or growth rates (157.7-250+ $\mu\text{mol kg}^{-1}$ Tables 2, 3 and Figures 1, 2).

3.2 *E. huxleyi* responses to temperature

5 The effect of temperature on rates was dependent upon CO_2 , with the greatest effect observed at optimum CO_2 concentrations (Figure 1). Increasing temperature increased maximum growth rates (V_{max}) up to twofold, photosynthetic rates up to 43% and calcification rates up to 52% (Figure 1, Table 2) under optimal CO_2 concentrations. CO_2 half saturation concentrations ($K_{\frac{1}{2}CO_2}^{sat}$) were insensitive to temperature (Table 2). However, under increasing temperatures CO_2 concentrations for both optimal growth and for inhibition of rates to half the maximum ($K_{\frac{1}{2}CO_2}^{inhib}$) decreased (Table 2).

10 3.3 *E. huxleyi* responses to light

Light intensities affected all physiological rates, with the greatest effect generally being observed at CO_2 concentrations at or above the optimum (Figure 2). Between 50 and 1200 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$, calcification rates doubled, photosynthetic rates tripled and growth rates increased around 36% (Figure 2, Table 3). Both optimum CO_2 and CO_2 concentrations at which rates were half saturated ($K_{\frac{1}{2}CO_2}^{sat}$) increased slightly with increasing light intensity (Table 3). CO_2 concentrations required to inhibit rates to half of maximum ($K_{\frac{1}{2}CO_2}^{inhib}$) for calcification and photosynthesis increased with increasing light intensity, while those for growth increased from 50-150 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ before decreasing with further increases in light (Table 3).

4 Discussion

4.1 Responses to changing carbonate chemistry: CO_2 and H^+

20 Rates of photosynthesis, calcification and growth in coccolithophores are strongly influenced by CO_2 (Bach et al., 2011; Sett et al., 2014; Zhang et al., 2015). Increasing CO_2 concentrations resulted in enhanced rates up to an optimum level beyond which they then declined again. This pattern in growth, photosynthetic carbon fixation and calcification rates has been observed previously for several coccolithophore species (Sett et al., 2014; Bach et al., 2015). The availability of substrate (CO_2 and HCO_3^-) was suggested as the factor influencing the increase in rates on the left side of the optimum, while the proton concentration ($[H^+]$) was the factor most likely driving declines to the right side of the optimum (Bach et al., 2011, 2015).

Of the two species, *E. huxleyi* has a higher CO_2 optimum than *G. oceanica* (Tables 2, 3 and S3, Gafar et al. 2018) for all rates and under most conditions. This could suggest that *E. huxleyi* has a slightly higher substrate requirement than *G. oceanica*. However, considering that *G. oceanica* has both a larger cell size and higher carbon quotas per cell the opposite would be expected (Sett et al., 2014; Bach et al., 2015). An explanation for achieving maximum rates only at higher CO_2 concentrations in *E. huxleyi*, in comparison to *G. oceanica* despite a lower inorganic carbon demand, might be a less efficient or capable

carbon uptake/ concentrating mechanism. Alternatively, a decreased sensitivity to high $[H^+]$ in *E. huxleyi*, in comparison to *G. oceanica* (see below), would lead to a shift in the optimum towards higher CO_2 as well and might be a more likely explanation.

Of the three rates, calcification in *E. huxleyi* had both the lowest CO_2 requirement and the highest sensitivity to increasing $[H^+]$ (Tables 3 and 2). This is a pattern previously observed for *G. oceanica* under varying temperature and light conditions (Gafar et al. 2018, See also Table S3). As evidenced by higher $K_{\frac{1}{2}CO_2}^{inhib}$ values for all processes, *E. huxleyi* also appears
5 less sensitive to the inhibiting effects of increasing $[H^+]$ than *G. oceanica* (i.e. $K_{\frac{1}{2}CO_2}^{inhib} = 47-250 \mu mol kg^{-1}$ versus $25-99 \mu mol kg^{-1}$ for *G. oceanica* depending on light intensities or $K_{\frac{1}{2}CO_2}^{inhib} = 62-250 \mu mol kg^{-1}$ versus $25-130 \mu mol kg^{-1}$ for *G. oceanica* depending on temperature) (Tables 2, 3, S3, Gafar et al. 2018). This also supports earlier results in a model analysis by Bach et al. (2015) where *E. huxleyi* reacted less sensitively to higher CO_2 (and $[H^+]$) than *G. oceanica*.

10 A lower sensitivity of rates to changes in carbonate chemistry speciation, in particular calcification rates, could be explained by the lower degree of calcification in *E. huxleyi* (PIC:POC ratios 0.24-1.38) when compared to *G. oceanica* (PIC:POC ratios 0.84-2.44) (Sett et al., 2014). Higher rates of calcification result in greater production of intracellular H^+ ($Ca^{2+} + HCO_3^- \rightleftharpoons CaCO_3 + H^+$), potentially decreasing $[CO_3^{2-}]$ in the coccolith producing vesicle and hence the $CaCO_3$ saturation state (Bach et al., 2015). Furthermore, increased $[H^+]$ has been found to result in declines in $[HCO_3^-]$ uptake, the primary carbon source
15 for calcification (Kottmeier et al., 2016).

4.2 Responses to temperature

Temperature was observed to have few modulating effects on CO_2 responses in *E. huxleyi*. **Changes in temperature produced little ($<1 \mu mol kg^{-1}$) change in CO_2 substrate half-saturation ($K_{\frac{1}{2}CO_2}^{sat}$) levels, at least within the measured range (Figure 1, Table 2). CO_2 requirements for optimum rates tended to slightly decrease with warming temperatures.** Similar results were
20 observed for *G. oceanica* (Gafar et al., 2018). This indicates that while overall rates change, carbon uptake mechanisms appear to scale to maintain internal substrate concentrations and thus cellular requirements regardless of temperature conditions.

In contrast, the inhibition of rates by rising $[H^+]$ i.e. $K_{\frac{1}{2}CO_2}^{inhib}$ was more sensitive to temperature. The CO_2 concentration at which rates were reduced to half the maximum increased with decreasing temperatures (Table 2). These results were also
25 observed for *G. oceanica* which had a lower sensitivity to increasing $[H^+]$ at the lowest tested temperature (Gafar et al., 2018). This also agrees with De Bodt et al. (2010) in which a greater decline in calcification rate was observed with increasing CO_2 at $18^\circ C$ than at $13^\circ C$. These results indicate that **at least some** coccolithophores may be less sensitive to high CO_2 levels at lower temperatures. As a result, both *G. oceanica* and *E. huxleyi* may become more vulnerable to the negative effects of ocean acidification as ocean temperatures increase due to climate change.

30 4.3 Responses to light

The sensitivity of all rates in *E. huxleyi* to changing carbonate chemistry, in particular increasing $[H^+]$, was clearly modulated by light intensity (Figure 2), agreeing with earlier findings (Zondervan et al., 2002; Feng et al., 2008; Gao et al., 2009; Rokitta and Rost, 2012; Zhang et al., 2015). CO_2 half-saturation ($K_{\frac{1}{2}CO_2 sat}$) for all rates were insensitive to increasing light intensities (Table S3). This agrees with results for *G. oceanica* which also displayed little change in CO_2 half-saturation concentrations with increasing light (Table S3). Increasing light intensity induced increases in CO_2 optima in all rates, however these changes were small ($<10 \mu mol kg^{-1}$) for calcification and growth rates. This contrasts with *G. oceanica* for which a distinct decrease in optimal CO_2 concentrations for growth rates with increasing light intensities was observed (Table S3). However, *G. oceanica* projections are based on a dataset with only three CO_2 concentrations ($\sim 16, 31, 45 \mu mol kg^{-1}$). As such, it is difficult to determine how robust the estimates of CO_2 optima and half-saturation requirements may be for this species (Zhang et al., 2015).

In *E. huxleyi* the relationship between H^+ sensitivity and light intensity was the same for the three rates. Calcification and photosynthetic carbon fixation and growth rates were most sensitive to H^+ at the lowest ($50 \mu mol photons m^{-2} s^{-1}$) and growth rates were also slightly more sensitive at the highest ($1200 \mu mol photons m^{-2} s^{-1}$) light intensities (Table 3). This result is in part due to an underestimation of growth rates by the fitting equation under high CO_2 conditions at $50 \mu mol photons m^{-2} s^{-1}$ light (Figure 2). However, it may be that sub-optimal light intensities add additional stress to the cells resulting in them having less resources with which to handle the stress of increasing high $[H^+]$. Hence rates are lower, but also appear more sensitive to changing carbonate chemistry. These findings agree with findings by Rokitta and Rost (2012) where a diploid *E. huxleyi* strain became insensitive to the effects of rising CO_2 (380 vs. 1000 μatm) when light intensities were increased from 50 to 300 $\mu mol photons m^{-2} s^{-1}$. However, this differs to *G. oceanica* which, with rising light intensities, had no change in sensitivity for calcification rates, a decrease in sensitivity for photosynthesis and an increase in sensitivity for growth rates (Table S3). Again, although this could be indicative for species specific differences in sensitivity, it may also be a result of the low number of CO_2 treatments used in the light data of *G. oceanica* (see Zhang et al. 2015).

4.4 *E. huxleyi* and *G. oceanica* a niche comparison

In the future ocean CO_2 , temperature and light availability are all expected to change (Rost and Riebesell, 2004; IPCC, 2013b). Levels of fCO_2 are expected to reach as high as 985 μatm by the end of the century with concomitant rise in global ocean temperature of up to 4.8°C (RCP8.5 scenario IPCC 2013a, b). Light intensities in the surface ocean are also expected to increase as a result of mixed layer depth shoaling (Rost and Riebesell, 2004). By calculating and comparing growth rates for *E. huxleyi* and *G. oceanica* over a range of environmental conditions, it is possible to differentiate between the fundamental (physiological) niche of a species and its potentially realised niche when in competition with others. For this purpose, light, temperature and CO_2 ranges were restricted to those where both species would be expected to co-occur, i.e. 20-1000 $\mu mol photons m^{-2} s^{-1}$, 8-30°C and 25-4000 μatm , respectively. The calculated difference in growth rates in response to CO_2 and temperature does

30 not significantly change with light intensity (Figure 3 and 4). It should be noted, however, that light intensity might modify observed growth rate differences for other strains of the same species than used here as they can possess different sensitivities and requirements (i.e. Langer et al. 2009; Müller et al. 2015).

4.4.1 Fundamental niche

Experimentally, *E. huxleyi* has been found to grow in a range of ~ 6 to $2500 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ with high light resulting in no inhibition of maximum rates in some strains, and up to 20% reduction in others (Balch et al., 1992; van Bleijswijk et al., 1994; Nielsen, 1995; Nanninga and Tyrrell, 1996; van Rijssel and Gieskes, 2002). In contrast, *G. oceanica* is more sensitive in a similar experimental range of ~ 6 - $2400 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ with maximum rates inhibited by up to 38% at high light intensities (Larsen, 2012). Light intensities below $6 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ for *E. huxleyi* and *G. oceanica* resulted in no growth for both species (van Bleijswijk et al., 1994; van Rijssel and Gieskes, 2002; Larsen, 2012). So, while *G. oceanica* is more sensitive to high light, the potential upper light limit for growth in both species is beyond naturally occurring maxima. Within this light range both species show a similar increase in projected absolute growth rates of 0-1.57 (d^{-1}) for *E. huxleyi* and 0-1.51 (d^{-1}) for *G. oceanica* (based on Figure 4).

10
E. huxleyi has been successfully cultured at $p\text{CO}_2$ levels between ~ 20 - $5600 \mu\text{atm}$, while *G. oceanica* has been successfully cultured at $p\text{CO}_2$ levels of ~ 20 - $3400 \mu\text{atm}$ (Sett et al., 2014). Again, the upper tolerance limit for growth in both is not known and well above what is expected for most ocean systems. Responses in projected growth rates with rising CO_2 differ between the two species with *G. oceanica* rates dropping to 50% of maximum at $f\text{CO}_2$ levels above $\sim 1760 \mu\text{atm}$ while *E. huxleyi* drops to 50% of maximum at $\sim 5950 \mu\text{atm}$. In terms of temperature *E. huxleyi* has a broader niche of 3 - 29°C in comparison to *G. oceanica* at 10 - 32°C . Within this temperature niche both species again show a similar change in absolute growth rates of 0-1.40 (d^{-1}) for *G. oceanica* and 0-1.43 (d^{-1}) for *E. huxleyi* (based on figure 5).

20 It should be noted however, that although niche ranges and maximum rates are similar for both species, different requirements ($K_{\frac{1}{2}\text{sat}}$) and sensitivities ($K_{\frac{1}{2}\text{inhib}}$) will lead to different actual rates at a specific environmental condition. This becomes evident when examining the temperature, light and CO_2 niches to find a combination of conditions at which growth rate for each species is at its maximum. For *E. huxleyi* maximum growth rates of 1.62 (d^{-1}) are projected at $\sim 970 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ light, $\sim 640 \mu\text{atm CO}_2$ and 20.2°C . In contrast, the conditions for optimal growth rates of 1.52 (d^{-1}) for *G. oceanica* are achieved at $\sim 500 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ light, $\sim 430 \mu\text{atm CO}_2$ and 24.4°C . Differences in sensitivity and therefore performance under certain conditions will influence the potentially realised niche of the species. For example, *E. huxleyi* is projected to reach higher growth rates than *G. oceanica* under a broader range of temperature, light and CO_2 conditions (Figures 3, 4 and 5), supporting the notion that *E. huxleyi* is rather a generalist.

4.4.2 Potentially realised niche

Temperature and CO₂ both have substantial effects on the potentially realised niche of *E. huxleyi* and *G. oceanica* (Figures 4 and 5). In contrast, light intensity has very little effect (Figure 3). *E. huxleyi* appears able to exceed growth rates of *G. oceanica* at temperatures below 22°C under most CO₂ and light conditions (Figures 4 and 5). A similar difference in temperature preferences has also been observed in New Zealand isolates of *Gephyrocapsa oceanica* and *Emiliania huxleyi* with *G. oceanica* and *E. huxleyi* growing between 10-25°C and 5-25°C at optimum temperatures of 22°C and 20°C, respectively (Rhodes et al., 1995). While these results are based on single strain laboratory experiments, there is evidence that such differences in temperature sensitivity may also hold true in the modern ocean. For example, data gathered from multiple phytoplankton monitoring cruises indicate that while both species are found at higher temperatures, *G. oceanica* largely vanishes from the assemblage at temperatures below 13°C (McIntyre and Bé, 1967; Eynaud et al., 1999; Hagino et al., 2005). However, phytoplankton monitoring cruises can be seasonally biased and represent a single point in time.

5

Another way to relate our niche comparison to today's oceans is through surface sediments. Surface sediment samples represent an integrated signal of the composition of a phytoplankton community over time and can therefore be a more suitable proxy of species dominance in a certain location. Global surface sediment data on *G. oceanica* and *E. huxleyi* coccolith abundance indicate that the dominance of these two species is influenced by temperature, particularly in the Pacific Ocean (Figure 6). It is noted, however, that samples from the south-equatorial to equatorial Atlantic Ocean in Boeckel et al. (2006) do not follow the general temperature trend observed in other ocean basins (Figure 6). In this location it appears that *G. oceanica* abundance is driven more by increasing nutrient concentrations than by temperature. It seems oceanic upwelling in this region is driving a different relationship between *E. huxleyi* and *G. oceanica* than observed in other areas. Globally the data suggests that dominance switches from *E. huxleyi* to *G. oceanica* at temperatures above 25°C which is similar to our projections. While both species have a similar upper limit to their fundamental thermal niche (i.e. Rhodes et al. 1995), it would appear that the higher minimum temperature of *G. oceanica*, combined with its greater tolerance for high temperatures, restricts its realised niche to the upper end of the temperature range (Figures 4 and 6).

CO₂ level also influences the relative growth rates of *E. huxleyi* and *G. oceanica*. Under current day levels of ~400 μatm, *E. huxleyi* would dominate at temperatures up to 22°C (Figure 5). However, at higher and lower CO₂ levels, *E. huxleyi* begins to outgrow *G. oceanica* at progressively higher temperatures. At the same time, combined warming in a future ocean would partially mitigate the higher CO₂ sensitivity of *G. oceanica* (Figure 5). Nevertheless, over the naturally observed temperature range, *G. oceanica*'s niche would be expected to decrease towards higher CO₂ levels.

25 This comparison only considers the responses of single strains of *E. huxleyi* and *G. oceanica*. Considering multiple strains, from diverse ocean regions, would aid our study in describing the fundamental and realised niches for a species in more general terms. However, even though our realised niche projections are based on only one strain for each species, they do

generally agree with experimental observations of other strains, and with planktonic and sediment observations of each species as a whole. This indicates that the differences in requirements and sensitivities of the two species as described here are large enough to be revealed by choosing only one representative for each species. Another consideration to be made is the fact that coccolithophore communities can be made up of dozens of species (McIntyre and Bé, 1967; Winter and Siesser, 1994), all of which are likely to have different preferences for and sensitivities to changes in $f\text{CO}_2$, temperature and light. Shifts in plankton community structure, as a result of different species and group preferences, in response to environmental change have already been observed in the past (Beaugrand et al., 2013; Rivero-Calle et al., 2015), while simulations also suggest shifts in plankton community under future climate conditions (Dutkiewicz et al., 2015). Community structure shifts and changes in coccolithophore species composition are likely to alter ocean biogeochemistry with implications for ocean-atmosphere CO_2 partitioning.

4.5 Global calcium carbonate production potential

The CaCO_3 production potential (CCPP) is based on cellular CaCO_3 quotas and growth rates calculated for a given set of temperature, light and carbonate chemistry conditions (see section 2.10). Here we test how this measure for productivity compares to estimated surface ocean CaCO_3 content observed by satellite imaging (PIC_s). At this point it is important to remember that CCPP does not account for top-down controls such as grazing or viral attack (Holligan et al., 1993; Wilson et al., 2002; Behrenfeld, 2014), and bottom-up controls such as competition for macro or micro-nutrients (Zondervan, 2007; Monteiro et al., 2016; Browning et al., 2017). Thus, a potential for high CaCO_3 production is not necessarily realised when exposed to different top-down and bottom up pressures.

Calculated CCPP of *E. huxleyi* alone (Figure 7) for the global ocean visually reproduces the mid-latitude production belts, however at lower latitudes than satellite PIC estimates. This agrees with the NEMO and OCCAM models of coccolithophore dominance (Sinha et al., 2010) and the chlorophyll a NASA Ocean Biogeochemical Model (NOBM) model for the Southern hemisphere and central North Atlantic provinces (Gregg and Casey, 2007). CCPP also estimates seasonal changes with higher productivity during summer in both hemispheres (see figure 7A and D vs. B and E). This pattern is driven mainly by temperature, which influences the latitudinal location of the bands, and light intensity, which influences whether the northern or southern band of productivity is stronger in a season. Nutrients are an essential, and in the ocean often limiting, requirement for biological productivity (Kattner et al., 2004; Browning et al., 2017). As such it would be expected that nutrients should also be strongly influencing seasonal patterns of PIC production. However, with the starting cell concentrations for the CCPP calculations chosen here, there was sufficient nitrate to support the projected production in most ocean regions (Figure 7C and F). High temperatures drove relatively low productivity in the equatorial regions in agreement with satellite PIC. Similar low levels of coccolithophores are estimated in Sinha et al. (2010) in the equatorial Pacific and Atlantic with the mixed phytoplankton functional group dominating with or without coccolithophores due to low iron and moderate phosphate concentrations and in Gregg and Casey (2007) for the equatorial Indian and Atlantic provinces. CCPP underestimates production at cold high latitudes, in particular in the Southern Ocean, when compared to the satellite. Similar low levels of coccolithophores

have been projected in the Southern Ocean in Gregg and Casey (2007) (very low coccolithophore chlorophyll a), Krumhardt et al. (2017) (growth rates at or close to zero which equates to low to zero CCPP) and Sinha et al. (2010) (high nutrients resulting in coccolithophores being dominated by diatoms). For the Southern Ocean, it has been suggested that satellite PIC concentrations in subantarctic waters are overestimated by a factor of 2-3 while those in Antarctic waters may be even more so (Holligan et al., 2010; Balch et al., 2011; Trull et al., 2018). The fact that three other global estimates, based on different sets of environmental parameters, all estimate very little PIC productivity in the Southern Ocean seems to support this theory. However, there are also specifically cold adapted strains of *Emiliania huxleyi* found at high latitudes which at least partially could explain discrepancies between the mentioned model projections and satellite derived PIC concentrations (see also below).

In Austral winter/Boreal summer CCPP (for *E. huxleyi*) and satellite PIC estimates closely match ($R^2=0.73$ $F=26.78$ $p<0.01$ $slope=1.03$) with low PIC in the South and central South provinces, very low PIC in the equatorial, North Indian and Antarctic provinces and higher PIC in the North central Pacific, North Pacific and North Atlantic provinces (Figure 8A). In Austral summer/Boreal winter CCPP (for *E. huxleyi*) and satellite PIC estimates in individual ocean provinces are also generally of overall good agreement but with a much lower slope ($R^2=0.85$ $F=50.01$ $p<0.01$ $slope=0.32$). Both CCPP and satellite PIC estimates for Austral summer/Boreal winter are low in all equatorial and North ocean provinces with slightly higher CCPP and satellite PIC production for the North central provinces and higher production in the South and South central provinces (Figure 8B). The reason for the relatively small slope of 0.32 in Austral summer, meaning that CCPP overestimates the total production by a factor of three, are the high values of satellite derived PIC in the Antarctic province. To rectify this issue, a simple scaling factor could be introduced.

Despite having similar PIC patterns, overall PIC estimates can differ significantly between CCPP and PIC_s in some provinces. These provinces can be divided into two groups characterized by either greater or lesser PIC estimates than those observed by satellite (Figure 8). The mid-latitude provinces of central South and central North Pacific and Atlantic and central South Indic in the summer season belong to the former, with higher CCPP than PIC_s. Recently, low phytoplankton biomass in these subtropical gyre systems have been hypothesized to be the result of strong grazing pressure despite high cellular growth rates (Behrenfeld, 2014), lending an explanation of why CCPP is higher than satellite PIC standing stocks. The lower PIC standing stocks estimated from the satellite could also be the result of other phytoplankton functional groups, such as diatoms, taking a comparatively bigger nutrient share (Iglesias-Rodríguez et al., 2002) thereby leaving less for PIC production by coccolithophores.

In contrast, in Austral summer/Boreal winter in the Antarctic and Austral winter/Boreal summer in the North Pacific, CCPP is smaller than satellite PIC estimates (Figure 8). *E. huxleyi*, which our projections are based off, has been found to dominate assemblages in polar areas, particularly in the southern hemisphere (Okada and Honjo, 1973; Gravalosa et al., 2008; Mohan et al., 2008; Charalampopoulou et al., 2016). The strains of *E. huxleyi* found here are special cold-adapted ones which can survive at temperatures as low as -1.7°C in the Antarctic (Cubillos et al., 2007) and -0.9°C in the Arctic (Charalampopoulou

et al., 2011)). As our CCPP is based on a temperate coccolithophore strain, lacking the cold adapted ones, our projections underestimate coccolithophore productivity in these areas. Additionally, differences in CCPP and satellite PIC in the Southern Ocean may also be connected to satellite overestimation of PIC at high southern latitudes (see above).

20

Comparing satellite PIC and CCPP in different oceanic provinces (Figure 8C) *E. huxleyi* alone provided the greatest agreement between both. The addition of *G. oceanica* to CCPP calculations negatively affected correlations with satellite PIC. This is counter-intuitive as one would expect increasing correlation of CCPP with satellite PIC as more species are used for the projection of the former. Indeed, estimates based on a combination of *E. huxleyi* and *G. oceanica* in Austral summer/Boreal winter were similar to those for *E. huxleyi* alone. However, in Austral winter/Boreal summer estimates based on a combination of *E. huxleyi* and *G. oceanica* resulted in much lower agreement between CCPP and satellite PIC when compared to *E. huxleyi* alone. This difference is driven by greatly increased CCPP estimates in the central North Pacific and Atlantic, combined with greatly decreased CCPP estimates in the North Pacific and Atlantic, relative to the *E. huxleyi* alone fit. Being a warm adapted species including *G. oceanica* would result in more productivity in the sub-tropical zones. However, these zones are also regions of potentially significant top-down control (see above for details). Meanwhile the North Pacific and Atlantic are likely dominated by cold-adapted species (see above for details), so including the warm-adapted *G. oceanica* in CCPP calculations would further reduce estimates in these regions. As a result, the inclusion of *G. oceanica* does not assist in making global estimates of coccolithophore PIC production.

30

5 Conclusions

Our analysis of the projected combination of increased temperature and CO₂ on potential success, in terms of growth rates, suggests that *E. huxleyi* will gain further competitive advantage over *G. oceanica*. Due to a greater sensitivity to CO₂, *G. oceanica*'s niche will likely contract to regions of higher temperature under future ocean conditions. In general, changes in community composition can influence community level carbon production and sequestration by coccolithophores. Such changes could have significant implications for climate feedback mechanisms, one being the relative strengths of the organic and inorganic carbon pumps in ecosystems where coccolithophores are abundant enough to significantly impact the air-sea CO₂ flux (e.g. coccolithophore blooms) and/or dominate the deep-sea flux of particulate material (e.g. subtropical gyres). Temperature and light were found to be important factors driving projections of CaCO₃ production potential (CCPP) on a global scale. Comparison of satellite derived inorganic carbon versus estimated inorganic carbon suggests that *E. huxleyi* CCPP is a good proxy for coccolithophore community production in most biogeographical provinces. However, results indicate that data on the responses of polar species and strains, to environmental change, may be required to improve estimates in the high-latitudes, while the effects of top-down controls might be needed to improve estimates in the mid-latitudes.

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10 *Data availability.* All data used for the calculation of model fits and coefficients for *Emiliana huxleyi* can be found in the supplementary material for this paper. Fit coefficients used for calculation of *Gephyrocapsa oceanica* niches can be found in Gafar et al. (2018) (DOI: 10.3389/fmars.2017.00433). Third party data sets used for calculation of global calcium carbonate production potential are detailed in Sect. 4.5

15 *Author contributions.* Conceived and designed the experiments: KS NG.
Performed the experiments: NG.
Analysed the data: NG KS.
Wrote the paper: NG KS.

Competing interests. The authors declare that they have no conflict of interest.

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References

- Andrulleit, H. and Rogalla, U.: Coccolithophores in surface sediments of the Arabian Sea in relation to environmental gradients in surface waters, *Marine Geology*, 186, 505–526, [https://doi.org/10.1016/S0025-3227\(02\)00312-2](https://doi.org/10.1016/S0025-3227(02)00312-2), 2002.
- 25 Andrulleit, H., Stäger, S., Rogalla, U., and Čepeck, P.: Living coccolithophores in the northern Arabian Sea: Ecological tolerances and environmental control, *Marine Micropaleontology*, 49, 157–181, [https://doi.org/10.1016/S0377-8398\(03\)00049-5](https://doi.org/10.1016/S0377-8398(03)00049-5), 2003.
- Bach, L. T., Riebesell, U., and Schulz, K. G.: Distinguishing between the effects of ocean acidification and ocean carbonation in the coccolithophore *Emiliania huxleyi*, *Limnology and Oceanography*, 56, 2040–2050, <https://doi.org/10.4319/lo.2011.56.6.2040>, 2011.
- Bach, L. T., MacKinder, L. C. M., Schulz, K. G., Wheeler, G., Schroeder, D. C., Brownlee, C., and Riebesell, U.: Dissecting the impact of CO₂ and pH on the mechanisms of photosynthesis and calcification in the coccolithophore *Emiliania huxleyi*, *New Phytologist*, 199, 121–134, <https://doi.org/10.1111/nph.12225>, 2013.
- Bach, L. T., Riebesell, U., Gutowska, M. A., Federwisch, L., and Schulz, K. G.: A unifying concept of coccolithophore sensitivity to changing carbonate chemistry embedded in an ecological framework, *Progress in Oceanography*, 135, 125–138, <https://doi.org/10.1016/j.pocean.2015.04.012>, 2015.
- 35 Balch, W., Drapeau, D., Bowler, B., Lyczkowski, E., Booth, E., and Alley, D.: The contribution of coccolithophores to the optical and inorganic carbon budgets during the Southern Ocean Gas Exchange Experiment: New evidence in support of the “Great Calcite Belt” hypothesis, *Journal of Geophysical Research: Oceans*, 116, C00F06, <https://doi.org/10.1029/2011JC006941>, 2011.
- Balch, W. M., Holligan, P. M., and Kilpatrick, K. A.: Calcification, photosynthesis and growth of the bloom-forming coccolithophore, *Emiliania huxleyi*, *Continental Shelf Research*, 12, 1353–1374, [https://doi.org/10.1016/0278-4343\(92\)90059-S](https://doi.org/10.1016/0278-4343(92)90059-S), 1992.
- Baumann, K.-H., Andrulleit, H., and Samtleben, C.: Coccolithophores in the Nordic Seas: Comparison of living communities with surface sediment assemblages, *Deep Sea Research Part II: Topical Studies in Oceanography*, 47, 1743–1772, [https://doi.org/10.1016/S0967-0645\(00\)00005-9](https://doi.org/10.1016/S0967-0645(00)00005-9), <http://www.sciencedirect.com/science/article/pii/S0967064500000059>, 2000.
- 5 Beaugrand, G., McQuatters-Gollop, A., Edwards, M., and Goberville, E.: Long-term responses of North Atlantic calcifying plankton to climate change, *Nature Climate Change*, 3, 263–267, <https://doi.org/10.1038/nclimate1753>, 2013.
- Behrenfeld, M. J.: Climate-mediated dance of the plankton, *Nature Climate Change*, 4, 880–887, <https://doi.org/10.1038/NCLIMATE2349>, 2014.
- 10 Bockmon, E. E. and Dickson, A. G.: A seawater filtration method suitable for total dissolved inorganic carbon and pH analyses, *Limnology and Oceanography: Methods*, 12, 191–195, <https://doi.org/10.4319/lom.2014.12.191>, 2014.
- Boeckel, B. and Baumann, K.-H.: Vertical and lateral variations in coccolithophore community structure across the subtropical frontal zone in the South Atlantic Ocean, *Marine Micropaleontology*, 67, 255–273, <https://doi.org/10.1016/j.marmicro.2008.01.014>, 2008.
- Boeckel, B., Baumann, K.-H., Henrich, R., and Kinkel, H.: Coccolith distribution patterns in South Atlantic and Southern Ocean surface sediments in relation to environmental gradients, *Deep Sea Research Part I: Oceanographic Research Papers*, 53, 1073–1099, <https://doi.org/10.1016/j.dsr.2005.11.006>, <http://www.sciencedirect.com/science/article/pii/S0967063706000045>, 2006.
- 15 Bopp, L., Monfray, P., Aumont, O., Dufresne, J.-L., Le Treut, H., Madec, G., Terray, L., and Orr, J. C.: Potential impact of climate change on marine export production, *Global Biogeochemical Cycles*, 15, 81–99, <https://doi.org/10.1029/1999GB001256>, 2001.
- Boyer, T. P., Antonov, J. I., Baranova, O. K., Coleman, C., Garcia, H. E., Grodsky, A., Johnson, D. R., Locarnini, R. A., Mishonov, A. V., and O’Brien, T. D.: World Ocean Database 2013, NOAA Atlas NESDIS 72, National Oceanographic Data Center, Silver Spring, MD, USA, <https://doi.org/10.2481/dsj.WDS-041>, 2013.
- 20

- Broecker, W. and Clark, E.: Ratio of coccolith CaCO_3 to foraminifera CaCO_3 in late Holocene deep sea sediments, *Paleoceanography*, 24, PA3205, <https://doi.org/10.1029/2009PA001731>, 2009.
- 25 Browning, T. J., Achterberg, E. P., Rapp, I., Engel, A., Bertrand, E. M., Tagliabue, A., and Moore, C. M.: Nutrient co-limitation at the boundary of an oceanic gyre, *Nature*, 551, 242–246, <https://doi.org/10.1038/nature24063>, 2017.
- Caldeira, K. and Wickett, M. E.: Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean, *Journal of Geophysical Research*, 110, C09S04, <https://doi.org/10.1029/2004jc002671>, 2005.
- Charalampopoulou, A., Poulton, A. J., Tyrrell, T., and Lucas, M. I.: Irradiance and pH affect coccolithophore community composition on a transect between the North Sea and the Arctic Ocean, *Marine Ecology Progress Series*, 431, 25–43, <https://doi.org/10.3354/meps09140>, 30 2011.
- Charalampopoulou, A., Poulton, A. J., Bakker, D. C., Lucas, M. I., Stinchcombe, M. C., and Tyrrell, T.: Environmental drivers of coccolithophore abundance and calcification across Drake Passage (Southern Ocean), *Biogeosciences*, 13, 5917, <https://doi.org/10.5194/bg-13-5917-2016>, 2016.
- Chen, M. and Shieh, K.: Recent nannofossil assemblages in sediments from Sunda Shelf to abyssal plain, South China Sea, *Proceedings of the National Science Council (ROC)*, Part A, 6, 250–285, 1982.
- 35 Cook, S. S., Whittock, L., Wright, S. W., and Hallegraeff, G. M.: Photosynthetic pigment and genetic differences between two Southern Ocean morphotypes of *Emiliania huxleyi* (Haptophyta), *Journal of Phycology*, 47, 615–626, <https://doi.org/10.1111/j.1529-8817.2011.00992.x>, 2011.
- Crafts-Brandner, S. J. and Salvucci, M. E.: Rubisco activase constrains the photosynthetic potential of leaves at high temperature and CO_2 , *Proceedings of the National Academy of Sciences*, 97, 13 430–13 435, <https://doi.org/10.1073/pnas.230451497>, 2000.
- Cubillos, J. C., Wright, S. W., Nash, G., De Salas, M. F., Griffiths, B., Tilbrook, B., Poisson, A., and Hallegraeff, G. M.: Calcification 5 morphotypes of the coccolithophorid *Emiliania huxleyi* in the Southern Ocean: Changes in 2001 to 2006 compared to historical data, *Marine Ecology Progress Series*, 348, 47–54, <https://doi.org/10.3354/meps07058>, 2007.
- De Bodt, C., Van Oostende, N., Harlay, J., Sabbe, K., and Chou, L.: Individual and interacting effects of $p\text{CO}_2$ and temperature on *Emiliania huxleyi* calcification: Study of the calcite production, the coccolith morphology and the coccosphere size, *Biogeosciences*, 7, 1401–1412, <https://doi.org/10.5194/bg-7-1401-2010>, 2010.
- 10 de Boyer Montégut, C., Madec, G., Fischer, A. S., Lazar, A., and Iudicone, D.: Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology, *Journal of Geophysical Research: Oceans*, 109, <https://doi.org/10.1029/2004JC002378>, 2004.
- Dickson, A. G.: Standards for ocean measurements, *Oceanography*, 23, 34–47, <https://doi.org/10.5670/oceanog.2010.22>, 2010.
- Dickson, A. G., Wesolowski, D. J., Palmer, D. A., and Mesmer, R. E.: Dissociation constant of bisulfate ion in aqueous sodium chloride 15 solutions to 250°C, *Journal of Physical Chemistry*, 94, 7978–7985, <https://doi.org/10.1021/j100383a042>, 1990.
- Dickson, A. G., Sabine, C. L., and Christian, J. R.: Guide to best practices for ocean CO_2 measurements, PICES Special Publication, North Pacific Marine Science Organization, Sidney, British Columbia, 2007.
- Doney, S. C., Fabry, V. J., Feely, R. A., and Kleypas, J. A.: Ocean acidification: The other CO_2 problem, *Annual Review of Marine Science*, 1, 169–192, <https://doi.org/10.1146/annurev.marine.010908.163834>, 2009.
- 20 Dutkiewicz, S., Morris, J. J., Follows, M. J., Scott, J., Levitan, O., Dyhrman, S. T., and Berman-Frank, I.: Impact of ocean acidification on the structure of future phytoplankton communities, *Nature Climate Change*, 5, 1002–1006, <https://doi.org/10.1038/nclimate2722>, 2015.

- Endo, H., Yoshimura, T., Kataoka, T., and Suzuki, K.: Effects of CO₂ and iron availability on phytoplankton and eubacterial community compositions in the northwest subarctic Pacific, *Journal of Experimental Marine Biology and Ecology*, 439, 160–175, <https://doi.org/10.1016/j.jembe.2012.11.003>, 2013.
- 25 Engel, A., Zondervan, I., Aerts, K., Beaufort, L., Benthien, A., Chou, L., Delille, B., Gattuso, J.-P., Harlay, J., Heemann, C., Hoffmann, L., Jacquet, S., Nejstgaard, J., Pizay, M.-D., Rochelle-Newall, E., Schneider, U., Terbruggen, A., and Riebesell, U.: Testing the direct effect of CO₂ concentration on a bloom of the coccolithophorid *Emiliana huxleyi* in mesocosm experiments, *Limnology and Oceanography*, 50, 493–507, <https://doi.org/10.4319/lo.2005.50.2.0493>, 2005.
- Eynaud, F., Giraudeau, J., Pichon, J.-J., and Pudsey, C. J.: Sea-surface distribution of coccolithophores, diatoms, silicoflagellates and dinoflagellates in the South Atlantic Ocean during the late austral summer 1995, *Deep-sea research. Part I: Oceanographic Research Papers*, 46, 451–482, [https://doi.org/10.1016/S0967-0637\(98\)00079-X](https://doi.org/10.1016/S0967-0637(98)00079-X), 1999.
- 30 Feng, Y., Warner, M. E., Zhang, Y., Sun, J., Fu, F.-X., Rose, J. M., and Hutchins, D. A.: Interactive effects of increased pCO₂, temperature and irradiance on the marine coccolithophore *Emiliana huxleyi* (Prymnesiophyceae), *European Journal of Phycology*, 43, 87–98, <https://doi.org/10.1080/09670260701664674>, 2008.
- 35 Feng, Y., Hare, C. E., Rose, J., Handy, S. M., DiTullio, G. R., Lee, P. A., Smith Jr, W. O., Peloquin, J., Tozzi, S., Sun, J., Zhang, Y., Dunbar, R. B., Long, M. C., Sohst, B., Lohan, M., and Hutchins, D. A.: Interactive effects of iron, irradiance and CO₂ on Ross Sea phytoplankton, *Deep Sea Research Part I: Oceanographic Research Papers*, 57, 368–383, <https://doi.org/10.1016/j.dsr.2009.10.013>, 2010.
- Fernando, A. G. S., Peleo-Alampay, A. M., and Wiesner, M. G.: Calcareous nannofossils in surface sediments of the eastern and western South China Sea, *Marine Micropaleontology*, 66, 1–26, <https://doi.org/10.1016/j.marmicro.2007.07.003>, 2007.
- Gafar, N. A., Eyre, B. D., and Schulz, K. G.: A conceptual model for projecting coccolithophorid growth, calcification and photosynthetic carbon fixation rates in response to global ocean change, *Frontiers in Marine Science*, 4, 1–18, <https://doi.org/10.3389/fmars.2017.00433>, 2018.
- 5 Gao, K., Ruan, Z., Villafane, V. E., Gattuso, J.-P., and Helbling, E. W.: Ocean acidification exacerbates the effect of UV radiation on the calcifying phytoplankter *Emiliana huxleyi*, *Limnology and Oceanography*, 54, 1855–1862, <https://doi.org/10.4319/lo.2009.54.6.1855>, 2009.
- Gravalosa, J. M., Flores, J.-A., Sierro, F. J., and Gersonde, R.: Sea surface distribution of coccolithophores in the eastern Pacific sector of the Southern Ocean (Bellingshausen and Amundsen Seas) during the late austral summer of 2001, *Marine Micropaleontology*, 69, 16–25, <https://doi.org/10.1016/j.marmicro.2007.11.006>, 2008.
- 10 Gregg, W. W. and Casey, N. W.: Modeling coccolithophores in the global oceans, *Deep Sea Research Part II: Topical Studies in Oceanography*, 54, 447–477, <https://doi.org/10.1016/j.dsr2.2006.12.007>, <http://www.sciencedirect.com/science/article/pii/S0967064507000318>, 2007.
- Guillard, R. R. L.: Culture of phytoplankton for feeding marine invertebrates, in: *Culture of Marine Invertebrate Animals*, edited by Smith, W. L. and Chanley, M. H., pp. 26–60, Plenum Press, New York, USA, 1975.
- 15 Hagino, K. and Okada, H.: Intra-and infra-specific morphological variation in selected coccolithophore species in the equatorial and sub-equatorial Pacific Ocean, *Marine Micropaleontology*, 58, 184–206, <https://doi.org/10.1016/j.marmicro.2005.11.001>, 2006.
- Hagino, K., Okada, H., and Matsuoka, H.: Coccolithophore assemblages and morphotypes of *Emiliana huxleyi* in the boundary zone between the cold Oyashio and warm Kuroshio currents off the coast of Japan, *Marine Micropaleontology*, 55, 19–47, <https://doi.org/10.1016/j.marmicro.2005.02.002>, <http://www.sciencedirect.com/science/article/pii/S0377839805000149>, 2005.
- 20

- Helm, D., Cook, S., Cubillos, J., McMinn, A., and Hallegraeff, G. M.: Growth, photosynthesis and temperature tolerance of eight Southern Ocean strains of the coccolithophorid *Emiliana huxleyi*, Masters thesis, Institute of Antarctic and Southern Ocean Studies, 2007.
- Henderiks, J., Winter, A., Elbraechter, M., Feistel, R., van der Plas, A., Nausch, G., and Barlow, R.: Environmental controls on *Emiliana huxleyi* morphotypes in the Benguela coastal upwelling system (SE Atlantic), Marine Ecology Progress Series, 448, 51–66, <https://doi.org/10.3354/meps09535>, http://www.int-res.com/articles/meps_oa/m448p051.pdf, 2012.
- Holligan, P. M., Fernández, E., Aiken, J., Balch, W. M., Boyd, P., Burkill, P. H., Finch, M., Groom, S. B., Malin, G., Muller, K., Purdie, D. A., Robinson, C., Trees, C. C., Turner, S. M., and van der Wal, P.: A biogeochemical study of the coccolithophore, *Emiliana huxleyi*, in the North Atlantic, Global Biogeochemical Cycles, 7, 879–900, <https://doi.org/10.1029/93GB01731>, 1993.
- Holligan, P. M., Charalampopoulou, A., and Hutson, R.: Seasonal distributions of the coccolithophore, *Emiliana huxleyi*, and of particulate inorganic carbon in surface waters of the Scotia Sea, Journal of Marine Systems, 82, 195–205, <https://doi.org/10.1016/j.jmarsys.2010.05.007>, 2010.
- Hutchinson, G.: Concluding remarks, Cold Spring Harbor Symposia on Quantitative Biology, 22, 415–427, 1957.
- Iglesias-Rodríguez, M. D., Brown, C. W., Doney, S. C., Kleypas, J., Kolber, D., Kolber, Z., Hayes, P. K., and Falkowski, P. G.: Representing key phytoplankton functional groups in ocean carbon cycle models: Coccolithophorids, Global Biogeochemical Cycles, 16, <https://doi.org/10.1029/2001GB001454>, 2002.
- IPCC: 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, 2013a.
- IPCC: Summary for policy makers, 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, edited by Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., V. B., and Midgley, P. M., pp. 1–27, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2013b.
- Kattner, G., Thomas, D. N., Haas, C., Kennedy, H., and Dieckmann, G. S.: Surface ice and gap layers in Antarctic sea ice: Highly productive habitats, Marine Ecology Progress Series, 277, 1–12, <https://doi.org/10.3354/meps277001>, <http://www.int-res.com/articles/meps2004/277/m277p001.pdf>, 2004.
- Kester, D. R., Duedall, I. W., Connors, D. N., and Pytkowicz, R. M.: Preparation of artificial seawater, Limnology and Oceanography, 12, 176–179, <https://doi.org/10.4319/lo.1967.12.1.0176>, 1967.
- Knappertsbusch, M.: Geographic distribution of living and Holocene coccolithophores in the Mediterranean Sea, Marine Micropaleontology, 21, 219–247, [https://doi.org/10.1016/0377-8398\(93\)90016-Q](https://doi.org/10.1016/0377-8398(93)90016-Q), 1993.
- Kottmeier, D. M., Rokitta, S. D., and Rost, B.: Acidification, not carbonation, is the major regulator of carbon fluxes in the coccolithophore *Emiliana huxleyi*, New Phytologist, 211, 126–137, <https://doi.org/10.1111/nph.13885>, 2016.
- Krumhardt, K. M., Lovenduski, N. S., Iglesias-Rodríguez, M. D., and Kleypas, J. A.: Coccolithophore growth and calcification in a changing ocean, Progress in Oceanography, 159, 276–295, <https://doi.org/10.1016/j.pocean.2017.10.007>, 2017.
- Langer, G., Nehrke, G., Probert, I., Ly, J., and Ziveri, P.: Strain-specific responses of *Emiliana huxleyi* to changing seawater carbonate chemistry, Biogeosciences Discussions, 6, 4361–4383, <https://doi.org/10.5194/bg-6-2637-2009>, 2009.
- Larsen, S. H.: Dimethylsulphoniopropionate (DMS) production of *Gephyrocapsa oceanica* in response to environmental forcing, Doctor of philosophy, School of Biological Sciences, Melbourne, <https://doi.org/10.4225/03/58a24e0331904>, 2012.
- Lefebvre, S. C., Benner, I., Stillman, J. H., Parker, A. E., Drake, M. K., Rossignol, P. E., Okimura, K. M., Tomoko, K., and Carpenter, E. J.: Nitrogen source and $p\text{CO}_2$ synergistically affect carbon allocation, growth and morphology of the coccolithophore *Emiliana huxleyi*:

- Potential implications of ocean acidification for the carbon cycle, *Global Change Biology*, 18, 493–503, <https://doi.org/10.1111/j.1365-2486.2011.02575.x>, 2012.
- Leibold, M. A.: The niche concept revisited: Mechanistic models and community context, *Ecology*, 76, 1371–1382, <https://doi.org/10.1111/j.1529-8817.2005.00152.x>, 1995.
- 25 Lewis, E., Wallace, D., and Allison, L. J.: Program developed for CO₂ system calculations, Carbon Dioxide Information Analysis Center, managed by Lockheed Martin Energy Research Corporation for the US Department of Energy Tennessee, Oak Ridge, https://doi.org/10.3334/CDIAC/otg.CO2SYS_DOS_CDIAC105, 1998.
- Longhurst, A. R.: Ecological geography of the sea, *Ecological Geography of the Sea Series*, Elsevier Science, London, UK, 2 edn., 2007.
- Lueker, T. J., Dickson, A. G., and Keeling, C. D.: Ocean pCO₂ calculated from dissolved inorganic carbon, alkalinity, and equations for K₁ and K₂: Validation based on laboratory measurements of CO₂ in gas and seawater at equilibrium, *Marine Chemistry*, 70, 105–119, 30 [https://doi.org/10.1016/S0304-4203\(00\)00022-0](https://doi.org/10.1016/S0304-4203(00)00022-0), 2000.
- McIntyre, A. and Bé, A. W. H.: Modern Coccolithophoridae of Atlantic Ocean -I. Placoliths and cyrtoliths, *Deep-Sea Research and Oceanographic Abstracts*, 14, 561–597, [https://doi.org/10.1016/0011-7471\(67\)90065-4](https://doi.org/10.1016/0011-7471(67)90065-4), 1967.
- Mohan, R., Mergulhao, L. P., Guptha, M. V. S., Rajakumar, A., Thamban, M., AnilKumar, N., Sudhakar, M., and Ravindra, R.: Ecology of coccolithophores in the Indian sector of the Southern Ocean, *Marine Micropaleontology*, 67, 30–45, 35 <https://doi.org/10.1016/j.marmicro.2007.08.005>, 2008.
- Moheimani, N. R. and Borowitzka, M. A.: Increased CO₂ and the effect of pH on growth and calcification of *Pleurochrysis carterae* and *Emiliana huxleyi* (Haptophyta) in semicontinuous cultures, *Applied microbiology and biotechnology*, 90, 1399–1407, <https://doi.org/10.1007/s00253-011-3174-x>, 2011.
- Monteiro, F. M., Bach, L. T., Brownlee, C., Bown, P., Rickaby, R. E., Poulton, A. J., Tyrrell, T., Beaufort, L., Dutkiewicz, S., and Gibbs, S.: Why marine phytoplankton calcify, *Science advances*, 2, e1501 822, <https://doi.org/10.1126/sciadv.1501822>, 2016.
- 5 Müller, M. N., Trull, T. W., and Hallegraeff, G. M.: Differing responses of three Southern Ocean *Emiliana huxleyi* ecotypes to changing seawater carbonate chemistry, *Mar. Ecol.-Prog. Ser.*, 531, 81–90, <https://doi.org/10.3354/meps11309>, 2015.
- Nanninga, H. and Tyrrell, T.: Importance of light for the formation of algal blooms by *Emiliana huxleyi*, *Marine ecology progress series*. Oldendorf, 136, 195–203, <https://doi.org/10.3354/meps136195>, 1996.
- NASA Goddard Space Flight Center, Ocean Ecology Laboratory, O. B. P. G.: Moderate-resolution Imaging Spectroradiometer (MODIS) Aqua Particulate Inorganic Carbon Data; 2014 Reprocessing, NASA OB.DAAC, Greenbelt, MD, USA, <https://doi.org/doi:10.5067/AQUA/MODIS/L3B/PIC/2014>, accessed 2/11/2017, 2014a.
- NASA Goddard Space Flight Center, Ocean Ecology Laboratory, O. B. P. G.: Moderate-resolution Imaging Spectroradiometer (MODIS) Aqua Photosynthetically Available Radiation Data; 2014 Reprocessing, NASA OB.DAAC, Greenbelt, MD, USA, <https://doi.org/10.5067/AQUA/MODIS/L3M/PAR/2014>, accessed 30/11/2017, 2014b.
- 15 Nielsen, M. V.: Photosynthetic characteristics of the coccolithophorid *Emiliana huxleyi* (Prymnesiophyceae) exposed to elevated concentrations of dissolved inorganic carbon, *Journal of Phycology*, 31, 715–719, <https://doi.org/10.1111/j.0022-3646.1995.00715.x>, 1995.
- Okada, H. and Honjo, S.: Distribution of coccolithophorids in the North and Equatorial Pacific Ocean: Quantitative data on samples collected during Leg 30, Oshoro-Mar, 1968 and Leg HK69-4, Hakuho-Mar, 1969, Report WHOI-73-81, Woods Hole Oceanographic Institution, Woods hole, Falmouth, unpublished manuscript, 1973.
- 20 Okada, H. and Honjo, S.: Distribution of Coccolithophores in Marginal Seas along the Western Pacific Ocean and in the Red Sea, *Marine Biology*, 31, 271–285, 1975.

- 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.-K., Rodgers, K. B., Sabine, C. L., Sarmiento, J. L., Schlitzer, R., Slater, R. D., Totterdell, I. J., Weirig, M.-F., Yamanaka, Y., and Yool, A.: Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms, *Nature*, 437, 681–686, <https://doi.org/10.1038/nature04095>, 2005.
- Paasche, E.: Roles of nitrogen and phosphorus in coccolith formation in *Emiliania huxleyi* (Prymnesiophyceae), *European Journal of Phycology*, 33, 33–42, <https://doi.org/10.1080/09670269810001736513>, 1998.
- Paasche, E.: A review of the coccolithophorid *Emiliania huxleyi* (Prymnesiophyceae), with particular reference to growth, coccolith formation, and calcification-photosynthesis interactions, *Phycologia*, 40, 503–529, <https://doi.org/10.2216/i0031-8884-40-6-503.1>, 2001.
- 25 Pascal, D.: GMIS - MERIS Monthly climatology sea surface diffuse attenuation coefficient at 490nm (9km) in m^{-1} , European Commission, Joint Research Centre (JRC), accessed 2/11/2017, 2013.
- Patil, S. M., Mohan, R., Shetye, S., Gazi, S., and Jafar, S.: Morphological variability of *Emiliania huxleyi* in the Indian sector of the Southern Ocean during the austral summer of 2010, *Marine Micropaleontology*, 107, 44–58, <https://doi.org/10.1016/j.marmicro.2014.01.005>, <http://www.sciencedirect.com/science/article/pii/S0377839814000085>, 2014.
- 30 Pörtner, H. O. and Farrell, A. P.: Physiology and Climate Change, *Science*, 322, 690–692, <https://doi.org/10.1126/science.1163156>, <http://www.sciencemag.org/content/322/5902/690.short>, 2008.
- Poulton, A. J., Adey, T. R., Balch, W. M., and Holligan, P. M.: Relating coccolithophore calcification rates to phytoplankton community dynamics: Regional differences and implications for carbon export, *Deep Sea Research Part II: Topical Studies in Oceanography*, 54, 538–557, <https://doi.org/10.1016/j.dsr2.2006.12.003>, 2007.
- Poulton, A. J., Charalampopoulou, A., Young, J. R., Tarran, G. A., Lucas, M. I., and Quartly, G. D.: Coccolithophore dynamics in non-bloom conditions during late summer in the central Iceland Basin (July-August 2007), *Limnology and Oceanography*, 55, 1601–1613, <https://doi.org/10.4319/lo.2010.55.4.1601>, 2010.
- 5 Powles, S. B.: Photoinhibition of photosynthesis induced by visible light, *Annual Review of Plant Physiology*, 35, 15–44, <https://doi.org/10.1146/annurev.pp.35.060184.000311>, 1984.
- Raven, J. A. and Crawford, K.: Environmental controls on coccolithophore calcification, *Marine Ecology Progress Series*, 470, 137–166, <https://doi.org/10.3354/meps09993>, 2012.
- 10 Rhodes, L. L., Peake, B. M., MacKenzie, A. L., and Marwick, S.: Coccolithophores *Gephyrocapsa oceanica* and *Emiliania huxleyi* (Prymnesiophyceae=Haptophyceae) in New Zealand's coastal waters: Characteristics of blooms and growth in laboratory culture, *New Zealand Journal of Marine and Freshwater Research*, 29, 345–357, <https://doi.org/10.1080/00288330.1995.9516669>, 1995.
- Riebesell, U., Zondervan, I., Rost, B., Tortell, P. D., Zeebe, R. E., and Morel, F. M. M.: Reduced calcification of marine plankton in response to increased atmospheric CO₂, *Nature*, 407, 364–367, <https://doi.org/10.1038/35030078>, 2000.
- 15 Rivero-Calle, S., Gnanadesikan, A., Del Castillo, C. E., Balch, W. M., and Guikema, S. D.: Multidecadal increase in North Atlantic coccolithophores and the potential role of rising CO₂, *Science*, 350, 1533–1537, <https://doi.org/10.1126/science.aaa8026>, 2015.
- Rokitta, S. D. and Rost, B.: Effects of CO₂ and their modulation by light in the life-cycle stages of the coccolithophore *Emiliania huxleyi*, *Limnology and Oceanography*, 57, 607–618, <https://doi.org/10.4319/lo.2012.57.2.0607>, 2012.
- 20 Rost, B. and Riebesell, U.: Coccolithophores and the biological pump: Responses to environmental changes, in: *Coccolithophores: From molecular processes to global impacts*, edited by Thierstein, H. R. and Young, J. R., book section 5, pp. 99–125, Springer, Berlin, Heidelberg, https://doi.org/10.1007/978-3-662-06278-4_5, 2004.

- Roth, P. H. and Coulbourn, W. T.: Floral and solution patterns of coccoliths in surface sediments of the North Pacific, *Marine Micropaleontology*, 7, 1–52, [https://doi.org/10.1016/0377-8398\(82\)90014-7](https://doi.org/10.1016/0377-8398(82)90014-7), 1982.
- 1130 Saavedra-Pellitero, M., Baumann, K.-H., Flores, J.-A., and Gersonde, R.: Biogeographic distribution of living coccolithophores in the Pacific Sector of the Southern Ocean, *Marine Micropaleontology*, 109, 1–20, <https://doi.org/10.1016/j.marmicro.2014.03.003>, 2014.
- Sabine, C. L., Feely, R. A., Gruber, N., Key, R. M., Lee, K., Bullister, J. L., Wanninkhof, R., Wong, C. S. I., Wallace, D. W. R., and Tilbrook, B.: The oceanic sink for anthropogenic CO₂, *science*, 305, 367–371, <https://doi.org/10.1126/science.1097403>, 2004.
- 1135 Samtleben, C. and Schroder, A.: Living coccolithophore communities in the Norwegian-Greenland Sea and their record in sediments, *Marine Micropaleontology*, 19, 333–354, [https://doi.org/10.1016/0377-8398\(92\)90037-K](https://doi.org/10.1016/0377-8398(92)90037-K), 1992.
- Schneider, U.: Influence of carbonate chemistry and light intensity on natural phytoplankton assemblages with emphasis on species composition, Doctor of philosophy, Biology/Chemistry, 2004.
- Schulz, K. G., Barcelos e Ramos, J., Zeebe, R. E., and Riebesell, U.: CO₂ perturbation experiments: Similarities and differences between dissolved inorganic carbon and total alkalinity manipulations, *Biogeosciences*, 6, 2145–2153, <https://doi.org/10.5194/bgd-6-4441-2009>, 2009.
- 1140 Schulz, K. G., Bach, L. T., Bellerby, R. G., Bermudez, R., Büdenbender, J., Boxhammer, T., Czerny, J., Engel, A., Ludwig, A., and Meyerhöfer, M.: Phytoplankton blooms at increasing levels of atmospheric carbon dioxide: Experimental evidence for negative effects on prymnesiophytes and positive on small picoeukaryotes, *Frontiers in Marine Science*, 4, 1–18, <https://doi.org/10.3389/fmars.2017.00064>, 2017.
- 1145 Sett, S., Bach, L. T., Schulz, K. G., Koch-Klavsen, S., Lebrato, M., and Riebesell, U.: Temperature modulates coccolithophorid sensitivity of growth, photosynthesis and calcification to increasing seawater pCO₂, *PLoS one*, 9, e88 308, <https://doi.org/10.1371/journal.pone.0088308>, 2014.
- Sharp, J. H.: Improved analysis for “particulate” organic carbon and nitrogen from seawater, *Limnology and Oceanography*, 19, 984–989, <https://doi.org/10.4319/lo.1974.19.6.0984>, 1974.
- 1150 Sinha, B., Buitenhuis, E. T., Le Quéré, C., and Anderson, T. R.: Comparison of the emergent behavior of a complex ecosystem model in two ocean general circulation models, *Progress in Oceanography*, 84, 204–224, <https://doi.org/10.1016/j.pocean.2009.10.003>, 2010.
- Takahashi, T., Sutherland, S. C., Chipman, D. W., Goddard, J. G., Ho, C., Newberger, T., Sweeney, C., and Munro, D.: Climatological distributions of pH, pCO₂, total CO₂, alkalinity, and CaCO₃ saturation in the global surface ocean, and temporal changes at selected locations, *Marine Chemistry*, 164, 95–125, <https://doi.org/10.1016/j.marchem.2014.06.004>, 2014.
- 1155 Trull, T. W., Passmore, A., Davies, D. M., Smit, T., Berry, K., and Tilbrook, B.: Distribution of planktonic biogenic carbonate organisms in the Southern Ocean south of Australia: a baseline for ocean acidification impact assessment, *Biogeosciences*, 15, 31–49, 2018.
- Uppström, L. R.: The boron/chlorinity ratio of deep-sea water from the Pacific Ocean, *Deep Sea Research and Oceanographic Abstracts*, 21, 161–162, [https://doi.org/10.1016/0011-7471\(74\)90074-6](https://doi.org/10.1016/0011-7471(74)90074-6), 1974.
- 1160 van Bleijswijk, J. D. L., Kempers, R. S., and Velhuis, M. J.: Cell and growth characteristics of types A and B of *Emiliania huxleyi* (Prymnesiophyceae) as determined by flow cytometry and chemical analysis, *Journal of Phycology*, 30, 230–241, <https://doi.org/10.1111/j.0022-3646.1994.00230.x>, 1994.
- van Rijssel, M. and Gieskes, W. W. C.: Temperature, light, and the dimethylsulfoniopropionate (DMSP) content of *Emiliania huxleyi* (Prymnesiophyceae), *Journal of Sea Research*, 48, 17–27, [https://doi.org/10.1016/S1385-1101\(02\)00134-X](https://doi.org/10.1016/S1385-1101(02)00134-X), 2002.

- 1165 Wilson, W. H., Tarran, G. A., Schroeder, D., Cox, M., Oke, J., and Malin, G.: Isolation of viruses responsible for the demise of an *Emiliana huxleyi* bloom in the English Channel, *Journal of the Marine Biological Association of the United Kingdom*, 82, 369–377, <https://doi.org/10.1017/S002531540200560X>, 2002.
- Winter, A. and Siesser, W. G.: Atlas of living coccolithophores, in: *Coccolithophores*, edited by Winter, A. and Siesser, W. G., vol. 13, book section 7, pp. 107–159, Cambridge University Press, Cambridge, United Kingdom, 1994.
- 1170 Winter, A., Jordan, R. W., and Roth, P. H.: Biogeography of living coccolithophores in ocean waters, in: *Coccolithophores*, edited by Winter, A. and Siesser, W. G., vol. 13, book section 8, pp. 161–177, Cambridge University Press, Cambridge, United Kingdom, 1994.
- Zhang, Y., Klapper, R., Lohbeck, K. T., Bach, L. T., Schulz, K. G., Reusch, T. B. H., and Riebesell, U.: Between-and within-population variations in thermal reaction norms of the coccolithophore *Emiliana huxleyi*, *Limnology and oceanography*, 59, 1570–1580, <https://doi.org/10.4319/lo.2014.59.5.1570>, 2014.
- 1175 Zhang, Y., Bach, L. T., Schulz, K. G., and Riebesell, U.: The modulating influence of light intensity on the response of the coccolithophore *Gephyrocapsa oceanica* to ocean acidification, *Limnology and Oceanography*, 60, 2145–2157, <https://doi.org/10.1002/lno.10161>, 2015.
- Zondervan, I.: The effects of light, macronutrients, trace metals and CO₂ on the production of calcium carbonate and organic carbon in coccolithophores - A review, *Deep Sea Research Part II: Topical Studies in Oceanography*, 54, 521–537, <https://doi.org/10.1016/j.dsr2.2006.12.004>, 2007.
- 1180 Zondervan, I., Rost, B., and Riebesell, U.: Effect of CO₂ concentration on the PIC/POC ratio in the coccolithophore *Emiliana huxleyi* grown under light-limiting conditions and different daylengths, *Journal of Experimental Marine Biology and Ecology*, 272, 55–70, [https://doi.org/10.1016/S0022-0981\(02\)00037-0](https://doi.org/10.1016/S0022-0981(02)00037-0), 2002.
- Zurell, D., Thuiller, W., Pagel, J., Cabral, J. S., Münkemüller, T., Gravel, D., Dullinger, S., Normand, S., Schifffers, K. H., and Moore, K. A.: Benchmarking novel approaches for modelling species range dynamics, *Global change biology*, 22, 2651–2664, 1185 <https://doi.org/10.1111/gcb.13251>, 2016.

Tables and Figures

Table 1. Fit coefficients (k_1 to k_6), R^2 , F-values, degrees of freedom and p-values obtained for calcification ($\text{pg C cell}^{-1} \text{d}^{-1}$), photosynthetic carbon fixation ($\text{pg C cell}^{-1} \text{d}^{-1}$) and growth rates (d^{-1}) from Eq. (2) fitted to data from this study and Sett et al. (2014). For calcification and photosynthetic carbon fixation rates the unit for $v = \text{pg C cell}^{-1} \text{day}^{-1}$ while for growth rates the unit for $v = \text{day}^{-1}$.

	Calcification	Photosynthesis	Growth
k_1 ($\text{pg C cell}^{-1} \text{day}^{-1}$ or day^{-1})	-11.98	-17.68	-0.71
k_2 ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)	-1.75E+06	-4.63E+06	-9.34E+05
k_3 ($\text{kg mol}^{-1} \mu\text{mol photons m}^{-2} \text{s}^{-1}$)	6.43E+07	1.39E+09	3.10E+08
k_4 ($\text{mol kg}^{-1} \text{ }^\circ\text{C}$)	-0.22	-0.23	-7.28E-02
k_5 ($^\circ\text{C}$)	28.14	26.72	-38.72
k_6 ($\text{kg mol}^{-1} \mu\text{mol photons}^{-1} \text{m}^2 \text{s }^\circ\text{C}^{-1}$)	-3.09E+03	4.40E+03	-2.70E+03
R^2 (p-value)	0.7957 (<0.001)	0.7302 (<0.001)	0.8460 (<0.001)
F-value (degrees of freedom)	389.51 (100)	273.52 (100)	552.74 (100)

Table 2. Optimum CO₂ concentrations, CO₂ K_{1/2} concentrations and maximum rates (V_{max}) at 10, 15 and 20°C from Eq. (2) fit to: CO₂-light data at 20°C in this paper and *E. huxleyi* CO₂ data from Sett et al. (2014) at 10°C, 15°C and 20°C and 150 μmol photons m⁻² s⁻¹ light intensity. Note that the CO₂ working range for the equation for this species was 0-250 μmol kg⁻¹. Values exceeding this range were reported as >250 μmol kg⁻¹.

CO ₂	10°C	15°C	20°C
CO₂ optima (μmol kg⁻¹)			
Calcification	16.94	12.91	11.50
Photosynthesis	20.34	15.42	13.91
Growth rate	29.06	20.78	18.36
V_{max}			
Calcification (pg C cell ⁻¹ d ⁻¹)	6.37	8.94	9.69
Photosynthesis (pg C cell ⁻¹ d ⁻¹)	8.55	11.52	12.22
Growth rate (d ⁻¹)	0.59	1.08	1.38
K_{1/2 CO₂} inhib (μmol kg⁻¹)			
Calcification	118.47	75.04	62.94
Photosynthesis	>250	119.54	100.51
Growth rate	>250	>250	192.74
K_{1/2 CO₂} sat (μmol kg⁻¹)			
Calcification	1.66	1.56	1.48
Photosynthesis	1.65	1.50	1.42
Growth rate	0.85	1.19	1.40

Table 3. Optimum CO₂ concentrations, CO₂ K_{1/2} concentrations and maximum rates (V_{max}) at 50-1200 μmol photons m⁻²s⁻¹ from Eq. (2) fit to: CO₂ data at 50, 400, 600 and 1200 μmol photons m⁻²s⁻¹ and 20°C in this paper and *E. huxleyi* CO₂ data from Sett et al. (2014) at 150 μmol photons m⁻²s⁻¹ light intensity and 10°C, 15°C and 20°C. Note that the CO₂ working range for the equation for this species was 0-250 μmol kg⁻¹. Values exceeding this range were reported as >250 μmol kg⁻¹.

CO ₂	50 PAR	150 PAR	400 PAR	600 PAR	1200 PAR
CO₂ optima (μmol kg⁻¹)					
Calcification	8.39	11.67	15.21	16.75	19.14
Photosynthesis	9.92	14.47	21.44	26.47	52.12
Growth rate	14.97	19.1	21.26	21.32	20.23
V_{max}					
Calcification (pg C cell ⁻¹ d ⁻¹)	7.64	10.05	12.47	13.48	15.04
Photosynthesis (pg C cell ⁻¹ d ⁻¹)	9.16	12.78	17.27	19.82	27.24
Growth rate (d ⁻¹)	1.19	1.43	1.58	1.61	1.62
K_{1/2 CO₂} inhib (μmol kg⁻¹)					
Calcification	47.38	63.01	80.19	87.68	99.10
Photosynthesis	73.04	104.90	182.32	>250	>250
Growth rate	157.71	208.62	206.04	192.60	163.64
K_{1/2 CO₂} sat (μmol kg⁻¹)					
Calcification	1.00	1.53	2.13	2.39	2.81
Photosynthesis	0.90	1.49	2.38	2.96	4.99
Growth rate	1.08	1.46	1.69	1.73	1.72

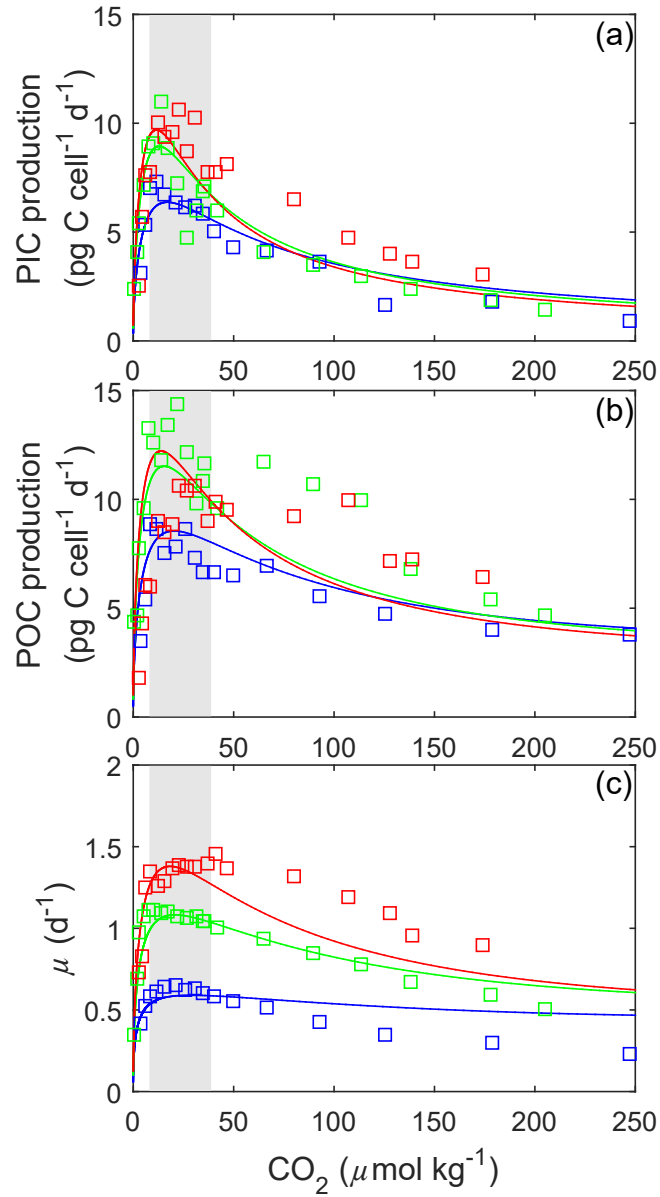


Figure 1. (A) Fitted particulate inorganic carbon (PIC), (B) particulate organic carbon (POC) production, and (C) growth rates (solid lines) of *E. huxleyi* in response to changes in carbonate chemistry at 10°C, 15°C and 20°C using Eq. (2) and fit coefficients from table 1. Symbols represent rate measurements from Sett et al. (2014) at 10°C, 15°C and 20°C and 150 μmol photons m⁻² s⁻¹. Shaded areas represent modern ocean CO₂ concentrations of 8.5-30 μmol kg⁻¹ based on data from Takahashi et al. (2014).

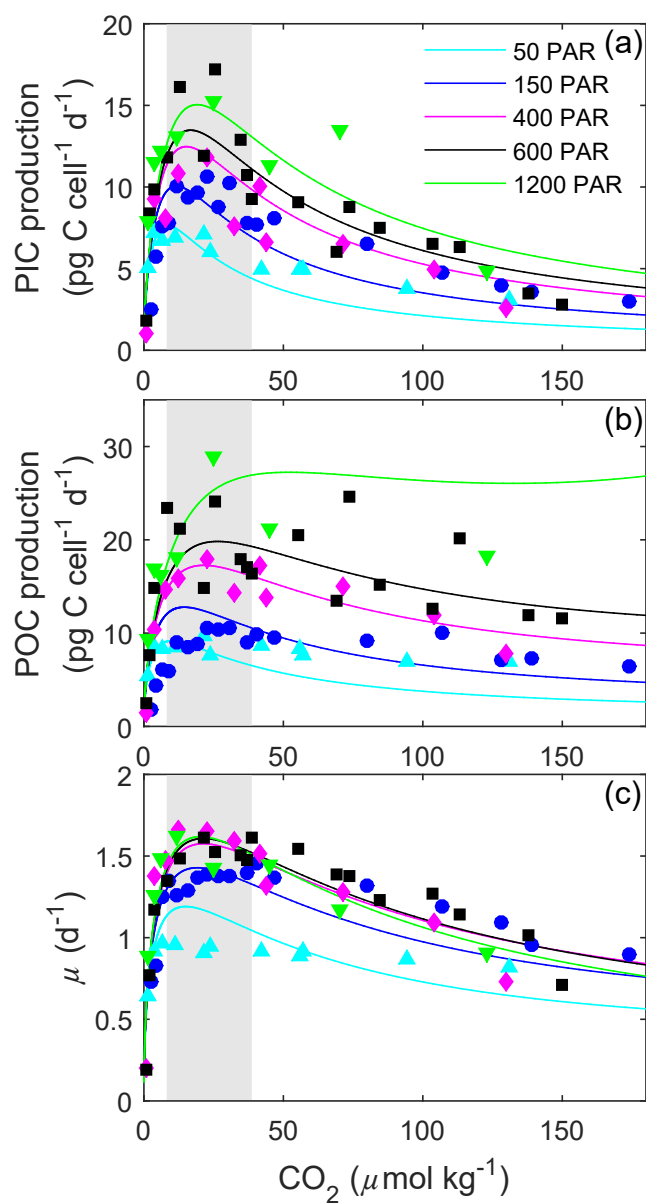


Figure 2. Fitted (solid lines) and measured (symbols) (A) particulate inorganic carbon (PIC) and (B) particulate organic carbon (POC) production, and (C) growth rates of *E. huxleyi* in response to changes in CO_2 concentration at six different light intensities using Eq. (2) and fit coefficients from table 1. Symbols represent rate measurements from this paper at a constant temperature (20°C) and 50, 150, 400, 600 and 1200 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$. Shaded areas represent modern ocean CO_2 concentrations of $8.5\text{-}30 \mu\text{mol kg}^{-1}$ based on data from Takahashi et al. (2014).

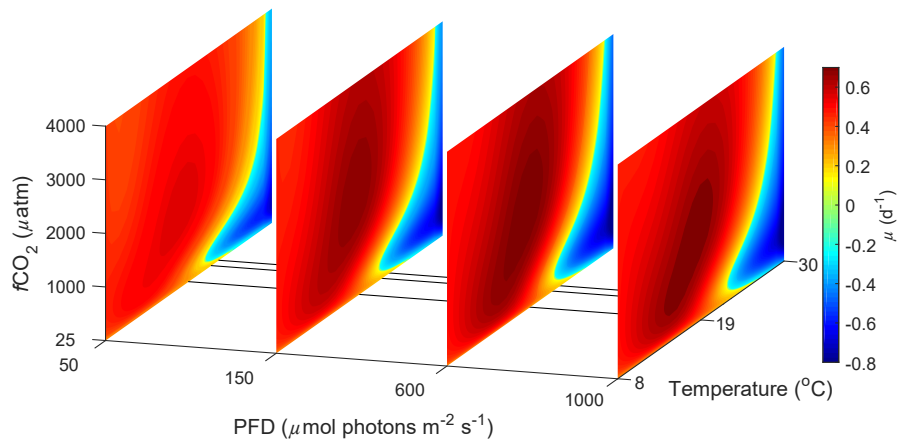


Figure 3. Predicted difference in growth rates between *E. huxleyi* and *G. oceanica* across a temperature range of 8-30°C and a $f\text{CO}_2$ range of 25-4000 μatm at 50, 150, 600 and 1000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ of PAR based on Eq. (2). Note the response to varying CO_2 or temperature is not significantly influenced by light intensity. Note positive values indicate *E. huxleyi* dominance while negative values indicate *G. oceanica* dominance.

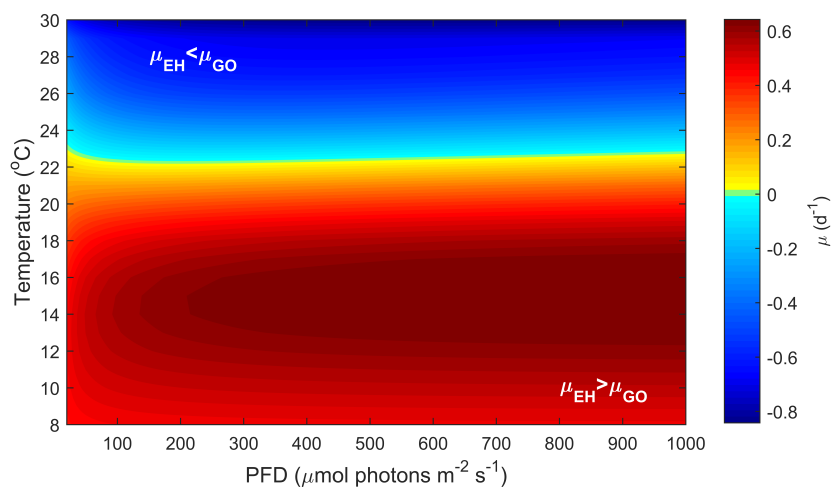


Figure 4. Predicted difference in growth rates between *G. oceanica* and *E. huxleyi* across a light range of 50-1000 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ and a temperature range of 8-30°C at 400 $\mu\text{atm } f\text{CO}_2$, based on Eq. (2).

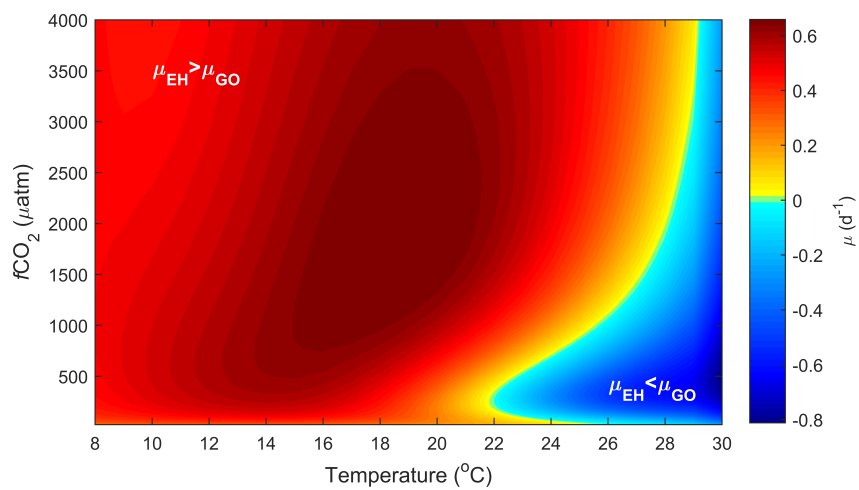


Figure 5. Predicted difference in growth rates between *E. huxleyi* and *G. oceanica* across a temperature range of 8-30°C and a $f\text{CO}_2$ range of 25-4000 μatm at $150 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ of light based on Eq. (2).

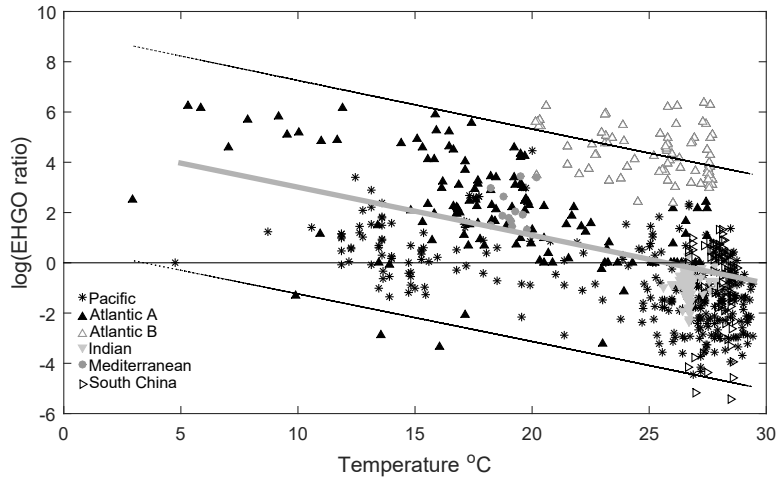


Figure 6. Log ratio of *E. huxleyi* to *G. oceanica* coccoliths versus temperature in the global oceans. Symbols and colours represent different ocean basins with data taken from McIntyre and Bé (1967); Chen and Shieh (1982); Roth and Coulbourn (1982); Knappertsbusch (1993); Andruleit and Rogalla (2002); Boeckel et al. (2006); Fernando et al. (2007); Saavedra-Pellitero et al. (2014). Symbols denote samples from different oceanic regions with Atlantic B specifically representing samples from Boeckel et al. (2006) which appear influenced by upwelling of nutrients (see section 4.4.2), while Atlantic A refers to samples from the Atlantic ocean from all other studies. The line at zero indicates a shift in dominance from *E. huxleyi* (>0) to *G. oceanica* (<0). The grey line represents a linear regression through the entire dataset with $p < 0.05$ and F of 156.05 with 95% prediction bounds for new observations. For details see Sect. 2.9.

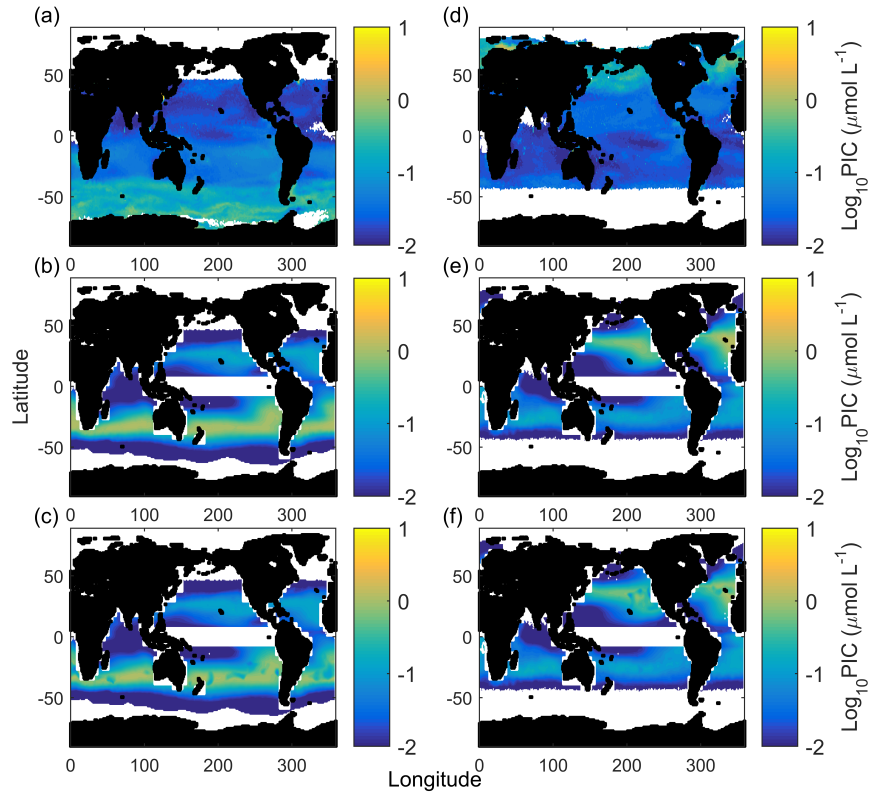


Figure 7. Austral summer/Boreal winter (A) and Austral winter/Boreal summer (D) satellite measured particulate inorganic carbon. Austral summer/Boreal winter (B) and Austral winter/Boreal summer (E) *E. huxleyi* based CCPP estimates accounting for carbonate chemistry (substrate and hydrogen ion concentrations), light intensity and temperature. Note the strong bands of CCPP at the mid-latitudes. Austral summer/Boreal winter (C) and Austral winter/Boreal summer (F) CCPP estimates accounting for carbonate chemistry (substrate and hydrogen ion concentrations), light intensity and temperature and nitrate concentrations (nutrient proxy).

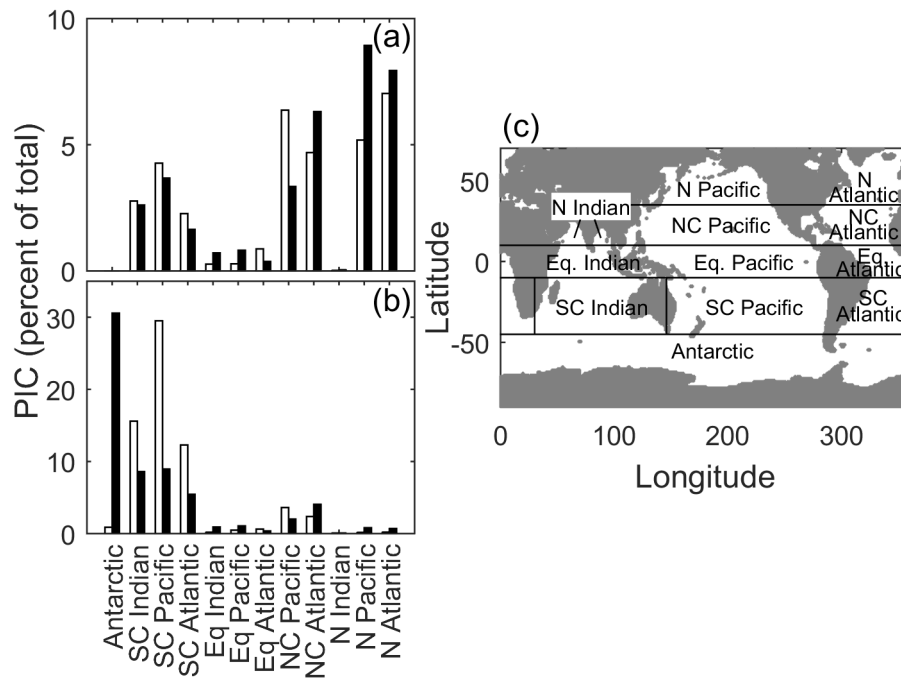


Figure 8. Satellite derived particulate inorganic carbon (black bars) and *E. huxleyi* based CCPP (white bars) estimates for major ocean biogeographical provinces as percentages of total production in (A) Austral winter/Boreal summer and (B) Austral summer/Boreal winter. (C) Major ocean biogeographical province definitions.