

Interactive comment on “Increasing coccolithophore abundance in the subtropical North Atlantic from 1990 to 2014” by K. M. Krumhardt et al.

Anonymous Referee #1

Received and published: 5 January 2016

GENERAL COMMENTS

The paper by Krumhardt et al. presents pigment and satellite derived data from the Bermuda Atlantic Time-Series (BATS) site in the subtropical North Atlantic to argue for an increase over time in the abundance of coccolithophores. The authors then use ancillary data from BATS to link this increase in coccolithophore 'abundance' to DIC and bicarbonate ion concentrations, and suggest that increases in these are causing increases in coccolithophore calcification, photosynthesis and growth. This is a potentially thought provoking study and could add to the growing debate on whether coccolithophores are responding positively or negatively to current changes in their growth

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habitat.

However, there are two fundamental and key assumptions in the paper by Krumhardt et al. which are highly questionable and unsupported by research – making the current conclusions of the paper unsound.

Assumption 1. Haptophyte pigment concentrations are an index for coccolithophore abundance (pg 18629, lns 26-29). Krumhardt et al. assume that all of the haptophyte pigment 19'-hexanoyl-oxyfucoxanthin (19'-hex) originates from coccolithophores. To support this key assumption they cite a paper which examined coccolithophore species composition at BATS (Haidar and Thierstein, 2001) from SEM analysis and ignored the full haptophyte community – this reference does not establish that coccolithophores dominate the haptophyte community in subtropical waters at BATS. (Note that the authors also cite the well-known book on coccolithophores by Thierstein and Young [2004], but is not clear in which chapter they find support for their assumption). Hence, the relative contribution of coccolithophores to total 19'-hex is unknown. The authors also completely ignore any potential effects of photo-acclimation (i.e. changes in pigment or chlorophyll per cell, or chlorophyll to carbon ratios) on pigment concentrations or pigment ratios (i.e. 19'-hex:Chlorophyll-a) – the high light/low nutrient concentrations in the upper 30 m at BATS will have significant impact on the cellular levels of pigments, and these will change with seasonal changes in light, nutrients, water-column stability and species composition. Hence, can the authors definitively say that the long-term trend is an increase in coccolithophore abundance and not an increase in either total haptophyte abundance or (cellular) pigment levels?

Assumption 2. Satellite derived PIC is reliable index for coccolithophore abundance. Satellite derived PIC reflects PIC from *E. huxleyi* rather than PIC from other species of coccolithophore – this is partly due to the high scattering from *E. huxleyi* coccoliths (e.g., Balch et al. 2005 J Geophys Res 110) and the propensity for this species to shed coccoliths into the surrounding water (i.e. the reflectance mostly comes from detached coccoliths rather than cells; Balch et al. 1996 Limnol Oceanogr). The detachment

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rate of *E. huxleyi* coccoliths from the coccosphere is dependent on growth rate and nutritional status. As coccoliths have negligible sinking rates, detached coccoliths (PIC) not associated with living cells can remain in the water-column after growing cells have dissipated (i.e. stopped growing or lost from the upper ocean via sinking, being eaten or viral lysis). Hence, it is extremely difficult to link the concentration of PIC with living coccolithophore biomass. Can the authors definitely say that the long-term trend is an increase in abundance and not an increase in the shedding of coccoliths into the water-column? Or a taxonomic change to a more *E. huxleyi* dominated community which has a greater propensity to shed coccoliths?

Supporting data (e.g., flow cytometry data on haptophyte abundances, counts of coccolithophores) is needed to fully validate the proxies (pigments, satellite PIC) used in this study. Considerable toning down of the paper could significantly alleviate the difficulties with interpreting the proxies used, and allow the paper a firmer scientific footing. For example, changing the title to a question (Are coccolithophores increasing in the subtropical N Atlantic?), presenting two lines of evidence (haptophyte pigments, satellite PIC), fully discussing the difficulty of interpreting the evidence (coccolithophore/haptophyte ratio, photo-acclimation, reflectance issues over PIC in low Chl waters, detrital PIC), the potential drivers (DIC, bicarbonate ions, nutrients, temperature etc – without circular arguments) and significantly rewording the conclusions.

SPECIFIC COMMENTS

Pg 18626, ln 11 – ‘coccolithophore pigment data’ – only coccolithophore pigment data? (see comments on interpretation of the haptophyte marker 19’hex)

Pg 18626, ln 16 (and throughout) – ‘coccolithophore abundance’ – the authors do not present abundance data (i.e. cell counts) or actual biomass (i.e. carbon), but rather present pigment concentration (absolute and relative) and satellite PIC (living and detrital biomass). Hence, the abstract and throughout the paper should be more specific when using the term abundance and reflect what the authors actually mean

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(pigments, chlorophyll-a, PIC).

Pg 18626, ln 17-18 – It is not obvious from the abstract that the study looked at anything other than DIC and bicarbonate ion – negative results relative to other growth-influencing factors (nutrients, light) should also be reported.

Pg 18627, ln 4 – Please explain what ‘a substantial fraction of the primary producers’ means – is this a substantial fraction of primary production, chlorophyll biomass, or cell abundance? What level is substantial (5% or 95%)?

Pg 18627, ln 20-21 – Bach et al. (2015) should also be referenced here for the substrate-inhibitor ratio argument. Also, these authors were very specific about the difficulties in applying this concept to field data when other growth limiting factors were varying – this limitation of the ratio should be mentioned here to highlight that coccolithophore growth in the natural environment is not just limited by bicarbonate/H⁺ (but nutrient and light availability).

Pg 18628, ln 9 – Consider replacing ‘challenging’ with ‘impossible’.

Pg 18628, ln 24 – Tyrrell and Taylor (1996) is part modelling and part model-field data comparison and hence this sentence should reflect that this reference is not just field data.

Pg 18629, ln 1 – Freeman and Lovenduski (2015) have no in situ field data – it is satellite derived – a better reference is needed (e.g. Feng et al. 2009 MEPS 388)

Pg 18629, lns 26-29 – This is a crucial assumption of the paper, which needs further validation and discussion. Neither of the references cited support that coccolithophores are the main component of the haptophyte community.

Pg 18630, ln 23 – More detail on the HPLC method for pigment detection at BATS is needed. Was it the same throughout? Did it change (and could this have changed the pigment ratios/signatures)? As the pigments are a major focus of the paper, much more methodological information is needed.

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Pg 18630, ln 26 – Letelier et al. (1993), although this reference is seminal it is also ~15 years old and there are many more papers on pigment ratios and using pigments to interpret phytoplankton community composition. Have the authors considered a more up to date reference with more up to date pigment ratios?

Pg 18631, ln 1 – ‘relatively constant ratios with total Chl-a’. What evidence is there that these ratios do not change with photo-acclimation and taxonomic shifts? Such potential problems should be discussed.

Pg 18635, ln 8-10 – It is surprising to find that *Prochlorococcus* is only found in the deep chlorophyll maximum – have the authors considered that this is an issue with their pigment ratios? There are two ecotypes of *Prochlorococcus*, one high-light living in surface waters and one low-light living around the DCM – the two have different (divinyl) chl-a to chl-b ratios whereas the authors (as in Letelier et al. 1993) only use one ratio (a deep *Prochlorococcus* ratio).

Pg 18642, ln 16 – The units on the estimated coccolithophore abundance are wrong – it should be 143×10^3 cells L⁻¹ and not 1.43×10^6 cells L⁻¹. Note that this is ~7 times higher than the average cell concentration (20×10^3 cells L⁻¹) determined from (SEM) cell counts by Haidar and Thierstein (2001) at BATS. This could be taken to imply that a large fraction of the haptophyte chlorophyll is not from coccolithophores, especially given that these estimates are based on *E. huxleyi* which only dominates in spring and other subtropical coccolithophore species may have much lower pigment content. It should also be noted that 100 coccolith coccospheres of *E. huxleyi* are rarely if ever seen outside of coccolithophore blooms or culture conditions.

Pg 18643, lns 20-22 – This line is a key statement underlining the difficulty of linking coccolithophore abundance with the growth environment and hence warrants more attention and discussion.

Section 4.4. Potential implications – this section is very speculative and could be summarised in a few lines (especially as there is little direct evidence at present that these

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changes are occurring).

Interactive comment on Biogeosciences Discuss., 12, 18625, 2015.

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