Reply to reviewers for manuscript entitled “Exceptional 2023 marine heatwave reshapes North Atlantic coccolithophore blooms”

Guinaldo & Neukermans

REV#2

The manuscript «Exceptional 2023 marine heat wave reshapes North Atlantic coccolithophore blooms» assesses the impact of North Atlantic coccolithophore blooms to both extreme events and long-term ocean warming. Using 25 years of satellite-derived particulate inorganic carbon data, the authors compare bloom dynamics in two regions; the Celtic Sea and the Barents Sea.

As I highlighted in the first round, the study is relevant because it provides valuable insights into carbon cycle responses to both long-term and extreme climatic events. I think that the authors have made a great effort to improve the manuscript from the previous iteration. My main complaints were that the article was primarily descriptive, and lacked clear indications of its contributions in terms of new data or methods. Additionally, some broad concepts were introduced without supporting information. I am glad to see that these flaws have been addressed.

However, I still think that terms such as Atlantification and acidification are not quantified, and might be something to explicitly address or indicate. I point here especially to expanding the discussion of the impacts of ocean acidification, which can be beneficial to contextualize long-term declines in the productivity of these calcifying organisms.

I also believe that the paper would benefit from disentangle the contributions of transient extreme events from those of persistent global warming. This may not be within the scope of the study but I think it would be valuable to include something less descriptive but more quantitative (maybe attribution methods, whose importance are recognized by the authors to distinguish the internal climate variability vs anthropogenic climate change).

I don’t have many specific comments: I believe the “Results” section should be “Results and Discussion”. The paragraph from lines 170 to 175 seems like conclusions rather than results nor discussion, and should be removed or moved. Following lines 194 to 196, I also wonder if the title of the paper should be reworded to include the long-term effects. Line 31 suggests that internal variability and long-term warming trends are the drivers of mhw

We would like to thank the reviewer for their comments on our article, for the time they spent reviewing it in detail, and for their help in improving it.

We fully agree that disentangling the contribution of extreme events from the long-term anthropogenic trend would be highly valuable. However, such attribution analyses are

currently very challenging in a biogeochemical context, particularly for PIC or coccolithophore-related variables. To our knowledge, formal detection–attribution frameworks have not yet been developed or applied robustly in ocean biogeochemistry, mainly because they require multi-decadal observational records combined with targeted model ensembles. For this reason, we remain limited to a descriptive interpretation of the respective roles of persistent warming and extreme events.

We propose a modified section in the discussion :

“Although attribution science has made substantial progress in recent years (Stott et al., 2016; Ribes et al., 2020; Faranda et al., 2024), these developments have focused primarily on terrestrial and atmospheric variables. In ocean biogeochemistry, formal attribution frameworks are still lacking, mainly because they require multi-decadal observations and dedicated model ensembles, which are not yet available for PIC variability. Developing attribution capabilities for marine biogeochemical systems would therefore require both multi-scale observation networks providing robust initial conditions and/or a solid observational “baseline” and improved modelling frameworks able to resolve subsurface dynamics and multi-stressor interactions (Gregg and Casey, 2007; Nissen et al., 2018; Krumhardt et al., 2019). Establishing such tools and datasets would be essential before the respective roles of internal variability, extreme events, and long-term anthropogenic forcing can be formally disentangled.”

Regarding the definition of the concept of Atlantification we modified the section starting on Line.126:

“Two distinct processes contribute to this warming: long-term ocean temperature increase, especially pronounced at high latitudes, and the enhanced influence/inflow of Atlantic Water, commonly referred to as “Atlantification.” (Årthun et al., 2012; Polyakov et al. 2017). In the Barents Sea, Atlantification encompasses not only a northward shift of the Polar Front, but also the progressive warming, increase of salinity, loss of winter sea ice, and modification of stratification conditions of waters on both sides of the front. While these changes are strongest south of the front, modified Atlantic water increasingly reaches the northern, traditionally Arctic domain, particularly during ice-free winters (Årthun et al., 2012). To disentangle these contributions, we tracked the annual position of the Polar Front, a proxy for the influence of Atlantic water (Fig. A7a; Neukermans et al., 2018).”

Regarding the acidification, we propose to expand the discussion section as requested:

“Coccolithophores are microscopic, calcifying phytoplankton that contribute to marine primary production and global carbon cycling through both the organic carbon and carbonate pumps (Rost and Riebesell, 2004 ; Neukermans et al. 2023). Ocean acidification, driven by increased CO_2 uptake, reduces carbonate ion availability and lowers pH, creating challenging chemical conditions for calcifying organisms (Riebesell et al 2000, Iglesias-Rodriguez et al 2008, Terhaar et al 2020}. Laboratory experiments show that impacts are dependent on the species. *Gephyrocapsa huxleyi* exhibits decreased calcification and lighter coccoliths under elevated CO_2, while other species may be more resilient but remain vulnerable to future acidification (Meyer et al 2015). Responses also

depend also on CO_2 enrichment which may allow partial compensation of calcification (Fukuda et al 2014). Global models project regionally heterogeneous effects, with some areas experiencing enhanced calcification due to carbon limitation alleviation, but a general decline is expected above ~600 µatm CO_2, with studies on long-term impacts suggesting progressive damages (Krumhardt et al. 2019, Tong et al. 2018}. Considering ocean acidification alongside warming and Atlantification provides essential context for interpreting the observed long-term declines in North Atlantic coccolithophore blooms."

References:

- Iglesias-Rodriguez, M. D., Halloran, P. R., Rickaby, R. E., Hall, I. R., Colmenero-Hidalgo, E., Gittins, J. R., ... & Boessenkool, K. P. (2008). Phytoplankton calcification in a high-CO2 world. *science*, *320*(5874), 336-340.
- Meyer, J., & Riebesell, U. (2015). Reviews and Syntheses: Responses of coccolithophores to ocean acidification: a meta-analysis. *Biogeosciences*, *12*(6), 1671-1682.
- Fukuda, S. Y., Suzuki, Y., & Shiraiwa, Y. (2014). Difference in physiological responses of growth, photosynthesis and calcification of the coccolithophore Emiliania huxleyi to acidification by acid and CO2 enrichment. *Photosynthesis research*, *121*(2), 299-309.
- Riebesell, U., Zondervan, I., Rost, B., Tortell, P. D., Zeebe, R. E., & Morel, F. M. (2000). Reduced calcification of marine plankton in response to increased atmospheric CO2. *Nature*, *407*(6802), 364-367.
- Tong, S., Gao, K., & Hutchins, D. A. (2018). Adaptive evolution in the coccolithophore Gephyrocapsa oceanica following 1,000 generations of selection under elevated CO 2. *Global Change Biology*, *24*(7), 3055-3064.

New title proposition : "Compounded effects of long-term warming and the exceptional 2023 marine heatwave on North Atlantic coccolithophore bloom dynamics"

We renamed the Results section "Results & Discussion". We also removed the lines 170-175.

REV#3

The authors present an observations-based study of coccolithophore blooms in two geographical domains, the Celtic Sea and the Baltic Sea, over the period 1998-2023, looking in particular for anomalies in 2023 corresponding to the marine heatwaves at that time.

Reviewers #1 and #2 were critical of many aspects in the original submission. They found many claims without references, and that several important terms and concepts were not well defined. Both reviewers described the paper as purely descriptive, contributing no new understanding of methods or concepts. In response, the authors have substantially revised their manuscript.

The revised paper appears to have addressed many of these criticisms. It is still a chiefly descriptive paper, but of a subject that is topical and relevant. As Reviewer #1 notes, it is a

decent documentation of the event and as an analysis it does have quality. It is clear that a lot of work has gone into the study. The paper contributes to our knowledge of the impact of marine heat waves on ecosystems, a subject that is topical and that we know too little of. The impact on coccolithophores is important for carbon uptake, as discussed in the paper. The impact of MHW more generally on algal blooms is also important for higher trophic levels, the wider ecosystem, and for commercial interests such as aquaculture. The study gives useful confirmation that the environmental ranges defined by O'Brien et al for coccolithophore blooms do seem to apply even in these anomalous MHW conditions and in two separate regions.

There is a lot of material in the appendix. I would prefer to see some of this moved to the main paper. As a reader, it can be frustrating to have to skip to the appendix to view information that is important in understanding key points in the paper. In particular figures A4 and A6, if that is allowed.

Thank you for this comment. We agree that Figures A4 and A6 contain important information, and we understand this comment. Because *Ocean Science Letters* has strict constraints on the length and structure of the main text, we need to confirm with the editor whether moving additional figures into the main manuscript is allowed.

In the following response, we accepted all suggestions unless a comment (in blue) indicated otherwise.

Below are more detailed comments on specific parts of the paper.

Line 13: replace "forms" with "form"

Section 2.1: This should mention the origin of the data sources used (SST, PAR, MLD). Details can be provided in the appendix but a brief mention is needed here. For explanation of O'Brien et al we are told to look at A1.4. Lines 309-313 of A1.4 give a very short explanation which could be moved here so that the reader doesn't have to jump.

To comply with the OS Letters guidelines, we prefer to keep the reference to the method in parentheses and keep the references as written in the manuscript.

Regarding the reference to Obrien's work, we noted the reviewer's comment. However, upon reading the two sections again, we feel that they complement each other and do not require any changes.

Section in the main text :

"To evaluate the impact of MHW on *G.huxleyi* blooms, we examine impacts on the three most influential environmental variables that characterize the ecological niches of coccolithophore species, namely SST, Photosynthetically Active Radiation (PAR), and the depth of the mixed layer (MLD), an indicator for the water column stratification (see Sect.A1.4; O'Brien et al 2016). For *G.huxleyi*, the optimal SST range was found to be situated between 6 and 16°C, optimal PAR between 35 and 42 Einstein.m−2.day−1}, and optimal MLD between 20 and 30 m (O'Brien et al., 2015). These ranges were extracted from the realized ecological niche of *G.huxleyi* (i.e. the environmental conditions under which it

can be observed) set up by (O'Brien et al., 2015), based on a global compilation of in situ measurements of coccolithophore species abundance and diversity (O'Brien et al., 2013)."

Section in Methods :

"Based on a global compilation of in situ measurements of coccolithophore species abundance and diversity (O'Brien et al., 2013), the realized ecological niche of G.huxleyi (i.e. the environmental conditions under which it can be observed) has been characterized (O'Brien, 2015). Out of seven environmental variables considered, O'Brien et al. (2016) showed that SST, PAR, and MLD were the most important variables influencing coccolithophore diversity. For G.huxleyi, the optimal SST range is situated between 6 and 16°C, optimal PAR between 35 and 42 Einstein.m−2.day−1, and optimal MLD between 20 and 30 m."

Lines 72, 73 and 90, 91: These have reminders of the ranges from O'Brien. Not needed.

In the first reviews received, reviewers suggested that references to conditions for blooms must be repeated for clarity. We therefore decided to maintain these references and reminders.

Line 77: "later" would be better than "onward"

Lines 81-84: Strictly, the NAO is just a number and doesn't drive turbulent mixing. Strong positive values of the NAO are associated with storms that do drive mixing. References to the NAO in this section do need to make clear when they are talking about positive or negative values of this index.

Thank you for this helpful comment. We agree that the NAO itself is an index and does not directly drive turbulent mixing. We have revised the text to clarify that it is the atmospheric conditions typically associated with positive (or negative) NAO phases that influence storminess, wind stress, and vertical mixing. The revised section now explicitly distinguishes between the NAO index and the physical mechanisms (e.g., westerlies, storm activity) that accompany its positive phase.

"In winter, the North Atlantic Oscillation (NAO) influences vertical turbulent mixing through the atmospheric conditions associated with its positive phase, which typically include enhanced westerlies and increased storm activity over the North Atlantic (Hurrell et al., 2003). Even at the northern edge of the North Atlantic, the BS atmospheric and oceanic internal variability responds to both positive and negative NAO conditions (Levitus et al., 2009; Chafik et al., 2015). In contrast, summer conditions favor the likelihood of high-pressure blocking systems over northern Europe (Rantanen et al., 2022; Rousi et al., 2022), characterized by weak winds and high solar radiation (Fig. A1, Fig. A2, Fig. A3)."

Line 87: replace "relations" with "relationship"

Line 87,88: I suggest deleting "the consequences of" Also, choose either "the persistent high-pressure system" or "persistent high-pressure systems" (no "the")

Line 97: “close to the normal winds” would be better without “the”.

Line 104: “fall” is repeated. Unless EGU editorial policy recommends American English, this should be “autumn”?

Line 111 mentions correlations shown in the appendix, table A1. It’s a very small table. Could these numbers please be moved into the main paper?

Thanks for this comment. We deleted the table and moved the numbers in the text.

“These levels were anomalously high in 2022 and 2023 (mean surface extent anomaly: 25 551 km2; maximum surface extent anomaly: 25 864 km2) and showed a significant correlation with spring–summer SSTs. Correlation coefficients reached 0.76 and 0.70 for mean and maximum surface extent, respectively, in relation to May–June SSTs, and 0.98 and 0.77 for mean and maximum surface extent, respectively, in relation to July–August–September SSTs (all p_value < 0.01).”

and

”In the BS, the increase in bloom extent was also strongly and significantly correlated with summer SSTs (Fig.A5b), with correlation coefficients of 0.95 and 0.96 for mean and maximum surface extent, respectively, in relation to July–August–September SSTs (p < 0.01). This highlights the role of warming in driving these changes.”

Line 118: “intrusion” implies that the coccolithophores have moved into the BS from the Atlantic. Is this what the authors mean? If so, it needs some evidence. If not, perhaps “expansion” would be a better word, as it’s neutral over whether the coccolithophores moved there or bloomed in situ.

We agree with this comment. We did not quantify the contribution of bio-advection (Oziel et al. 2020) and *in situ* proliferation. However, if we replace “intrusion” by “expansion” we will have a sentence containing two occurrences of the word “expansion.” We therefore propose the following sentence:

“This reflects a northeastward expansion of coccolithophores in the BS linked to the shifting polar front.”

Line 120 and Figure 3 mention LOESS. As an acronym it needs expanding the first time it’s used. Maybe even a citation such as Cleveland 1979? https://doi.org/10.1080/01621459.1979.10481038

“Over the past 25 years, Locally Estimated Scatterplot Smoothing regression (LOESS, Cleveland, 1979) reveals significant positive trends in bloom extent”

Line 126 talks about Atlantification. As the other reviewers noted, it would be useful to describe what this word means. I guess that water on both sides of the Polar Front is becoming more “Atlantic”? This might be worth mentioning, so that we don’t view Atlantification as just being a northward shift in the Polar Front.

Thank you for this comment. We agree that “Atlantification” should be defined more precisely. In the Barents Sea, it does not only correspond to a northward shift of the Polar Front, but also to an increasing inflow of Atlantic Waters in the sea. While the effects are strongest south of the front, Atlantic Water increasingly reaches the Arctic region, particularly during ice-free winters, affecting surface and subsurface conditions. We have clarified this in the text.

“Two distinct processes contribute to this warming: long-term ocean temperature increase, especially pronounced at high latitudes, and the enhanced influence/inflow of Atlantic Water, commonly referred to as “Atlantification. (Årthun et al., 2012; Polyakov et al., 2017). In the BS, Atlantification encompasses not only a northward shift of the Polar Front, but also the progressive warming, increase of salinity, loss of winter sea ice, and modification of stratification conditions of waters on both sides of the front. While these changes are strongest south of the front, modified Atlantic water increasingly reaches the northern, traditionally Arctic domain, particularly during ice-free winters (Årthun et al., 2012). To disentangle these contributions, we tracked the annual position of the Polar Front, a proxy for the influence of Atlantic water (Fig. A7a; Neukermans et al., 2018).”

Caption for Figure 3: In the final sentence, replace “indicated” with “indicate”.

Line 138: “hinder” isn’t quite the right word. “disregard” would be better.

Line 143: replace “a shift” with “an eastward shift”

Line 144: I suggest replacing “front positions have” with “front position has” Also, replace “another value close to the record high” with “a value close to the maximum”

Line 151: replace “revealed” with “reveals”, “both” with “the two” (else you are saying that each region independently has dynamics that contrast with itself)

Line 156: Suggest delete “despite interannual variability”

Lines 156-157: replace “seems to imprint” with “gives”

Line 159: “durations” should be singular

Line 160: the 2nd “mid-June” needs deleting?

Lines 168-169: The sentence beginning “In both regions” doesn’t read very well and needs rewriting. I suggest: “Positive stratification anomalies were recorded in both regions in 2023, with the CS reaching record levels, which supported favourable conditions for G. huxleyi."

Thanks. This sentence has been changed accordingly.

Line 174: replace “analyses” with “analysis”

Line 178: suggest deleting “oceanic”

Line 179: suggest deleting “dedicated”

Line 187: suggest deleting “within the 6-16oC range”. Either that or add a range for PAR, so that SST and PAR are given consistently.

Lines 192-193: Suggest deleting the sentence “In addition...” It feels out-of-place as this paper is not about wider ecosystem responses or adaptation plans and policies. If the authors did want to keep this sentence then the paper really needs more text on this subject.

Lines 200-202: Suggest deleting from “and combine” to the end of the sentence. Again, this opens a new topic that would need more text. For instance, can we really believe that numerical simulations of coccolithophore blooms will “accurately quantify the contributions of the respective processes”? I understand that it is a suggestion for further work, but I think it isn’t needed and that the science isn’t yet able to comply.

Line 205: suggest “due to masking by cloud cover” to make clear how cloud cover affects the satellite estimates

Lines 209-210: suggest replacing “vertically resolved” with “sub-surface” which has clearer meaning

Line 215: The sentence beginning “Additionally...” doesn’t completely make sense after the word “Atlantic”.

Mention of impacts on regional carbon cycle in the next sentence so we remove the mention in this sentence. The new sentence is the following : “Additionally, the evolution of water column stratification plays a key role in promoting blooms with a clear signal in the North Atlantic.”

Lines 218-221: Do we know the impact of these blooms on the regional ocean carbon cycle? If not, you might delete from “Knowing” up to the first comma?

Thank you for the comment. A few studies have attempted to quantify the impact of coccolithophore blooms on the regional carbon cycle, including their effects on surface pCO_2, air–sea CO_2 fluxes, primary production, calcification, and carbon export via the calcite ballast effect. This quantification remains challenging. To expand on this point, we have revised the sentence and added key references documenting these impacts :

- Shutler, J. D., Land, P. E., Brown, C. W., Findlay, H. S., Donlon, C. J., Medland, M., ... & Blackford, J. C. (2013). Coccolithophore surface distributions in the North Atlantic and their modulation of the air-sea flux of CO 2 from 10 years of satellite Earth observation data. *Biogeosciences*, *10*(4), 2699-2709.
- Rigual Hernández, A. S., Trull, T. W., Nodder, S. D., Flores, J. A., Bostock, H., Abrantes, F., ... & Northcote, L. C. (2020). Coccolithophore biodiversity controls carbonate export in the Southern Ocean. *Biogeosciences*, *17*(1), 245-263.
- Delille, B., Harlay, J., Zondervan, I., Jacquet, S., Chou, L., Wollast, R., ... & Gattuso, J. P. (2005). Response of primary production and calcification to changes of pCO2 during experimental blooms of the coccolithophorid Emiliania huxleyi. *Global Biogeochemical Cycles*, *19*(2).

- Klaas, C. & Archer, D. E. Association of sinking organic matter with various types of mineral ballast in the deep sea: Implications for the rain ratio. *Glob. Biogeochem. Cycles* **16**, 63-1–63–14 (2002).

Section modified :

"Coccolithophore blooms can influence the regional ocean carbon cycling by modifying surface pCO_2 through the combined effect of primary production and calcification air–sea CO_2 exchange, and carbon export and deep particle fluxes through the calcite ballast effect (Shutler et al., 2013; Delille et al., 2005; Klaas & Archer, 2002; Rigual Hernández et al., 2020). Understanding and disentangling these influences on carbon cycling now and in the future is therefore crucial, especially as any potential long-term weakening of the ocean carbon sink may compound with short-term decline associated with MHW events (Muller et al 2025)."

Line 222: suggest deleting "and reaching exceptional level". The next words ("are an extreme signature") give the same message and sound better.

Lines 245-246: suggest "...where blooms occur annually and marine heat waves resulted in..."

Line 270: "in a regular" should be "on a regular"

Line 278: Can the authors explain why March-April SSTs are used for estimating the Polar Front?

As referenced in Neukermans et al (2018), the position of the SST front in March–April is a good indicator for the annual extent of Atlantic waters as the water column is vertically well mixed and the Atlantic waters are not yet stratified.

Lines 283:285: "To evaluate..." No need to mention this evaluation unless you quote results from it.

Thanks for this. Sentence modified : Vertical temperature and the stratification are derived from the Institute of Atmospheric Physics (IAP) observation-based temperature/salinity fields at 1°x1° horizontal resolution and 41 vertical levels from 1-2000m and a monthly resolution from January 1940 to September 2023 were used.

Figure A9: I found this figure hard to interpret. Wouldn't a timeseries plot be clearer?

Thank you for this suggestion. In this figure, we show the annual maxima of PIC, so the temporal resolution is already yearly rather than continuous. For this type of discrete annual information, we believe a barcode representation is more appropriate than a lineplot.

Table A1: Please explain that MJ and JAS indicate months. All the values in the table have *** to indicate p value < 0.01 Suggest adding a comment that they are all significant at this level, and omitting the *** Suggest also explaining why no values were calculated for BS for May-June.

In a previous comments, Rev#3 asked to remove this table and add the numbers in the text.