

Reply to reviewer for “Exceptional 2023 marine heatwave reshapes North Atlantic coccolithophore blooms”

REV#1

The authors present a brief descriptive study of the 2023 marine heat waves in the Northeast Atlantic, with two case studies in the Celtic and Barents seas. I found the study to be a decent documentation of this event and I acknowledge the quality of the analysis.

However, I am quite annoyed by the form of the study. Is there a limit to the “fast-science” ? and to the fact of hastily producing a piece of paper with huge or vague statements not specific enough or NOT supported by results ? It’s a paper which does not produce any data, new methods or concepts and does not study any process. This is purely descriptive, which would be fine in principle, if the authors would stick to interpreting their results. But this article is greedy and illegitimately intended to be as wide-ranging as possible, mentioning as many buzzwords and fancy concepts as possible (acidification = no analysis, Atlantification = not even defined, poleward expansion = not quantified at all although the authors conclude about a spatial shift.... , ecological niche/hotspots = not defined + not quantified, emergence = not defined/quantified, top-down controls = not analyzed, bottom-up controls = not analyzed, for example, there are interpretations of the role of light without any analysis of light/PAR; or the role of atmospheric conditions with no analysis of atmospheric conditions, sea-ice and ocean currents are mentioned many times also without any result shown).

The fact that they give advice on what people should do next in term of observation and modelling is already annoying, but fine. What is least acceptable is that, in most cases, the claims are not backed up by results. Furthermore, on top of those concepts that are discussed without any analysis, many aspects of the methods are incomplete (see point-by-point comments below: undefined/unprecise concepts: climate variability, Atlantification, optimal bloom development zones ?, trailing/leading regions ? ; incomplete references; missing methods: extent of the bloom ?, leading edge ?, thermal range of coccos?). Many assertions are (most of the time true) but baldly claimed, not even backed up by any references. Due to this bad referencing, the authors presume the reader is an expert (otherwise it’s a very complicated read through although it is written quite succinctly) and oblige the reader to look back-and-forth for the needed information throughout the manuscript (many times introduced way after being used: e.g. upper thermal range, never explained).

I also raise a few formal points, i.e. some wording so as not to overstate -sell- the overall importance of E. Huxleyi in the carbon cycle and also in the trophic chain. There is no evidence that they contribute

significantly to the BCP beyond the “ballast effect”, as they contribute to a small (~10%) share of the total biomass and the total BCP, release CO₂ during calcification, and they are generally avoided by grazers.

Too much is too much, I recommend the authors to take the time to fix this study and to re-submit later on and spare the energy of the readers. A great deal of work is needed before authors can provide analysis to back up all their assertions. An easier alternative would of course be to clarify, or indicate the source of their unsupported results, and/or (re)move them into the discussions.

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. The reviewer raised important issues, which we have addressed by adding new figures and analyses to the revised version. We believe that these changes will address his/her concerns. Due to the extent of the work involved, some comments are not addressed point by point, as we decided to revise most sections. In particular, we have added references on the ecological niches of *G. huxleyi* and proposed an analysis of PAR and polar front trends during the satellite era. This has allowed us to demonstrate the key role of extreme heat events in intensifying blooms.

DETAILED COMMENTS:

METHODS:

Extent of the bloom: I find it not straightforward to understand how the mean/max of the extent of the bloom is derived. Do I understand properly that the bloom start/end is calculated following Hopkins et al. 2015 (with you own custom criterions) pixel by pixel with daily images ? Right ? So the mean/max you are displaying are temporal ? Of daily maps or aggregated monthly maps ? I doubt daily maps have enough coverage to derive a bloom extent, at least in the BS. Also, In which time windows (I guess not the whole year, only the bloom period I guess) ? Maybe try to be more specific in the A1.3.

In this study, we computed regional thresholds based on daily values. We then applied these thresholds to weekly merged products to determine the weekly extent. We applied this method to the entire year, but only weeks within the proliferation period show surface extent.

Sentence in the Methods section :

“The surface extent computation relies on the number of relevant pixel areas detected with a PIC concentration greater than a region-based threshold (defined on daily products) applied to the weekly-merged L3 products.”

INTRODUCTION

Lines 25-26 – I thought thin strain has been renamed “*Gephyrocapsa huxleyi*”. Please double-check and eventually fix it. The authors acknowledged the relative small contribution of coccos to the global NPP Line

23 (although I would appreciate some references here). Is the 1-10% contribution is for actually *E. huxleyi* or for coccolithophores in general? Verify. Same for PIC, orders of magnitudes compared to other carbonated-shell species would help rather than using non-quantitative adjectives such as “important” or “significant” (there are repetitions by the way).

The reviewer is correct that the species “*Emiliania huxleyi*” has been recently renamed “*Gephyrocapsa oceanica*”. Thank you for pointing that out; it escaped our attention. We have replaced every occurrence of *Emiliania huxleyi* with *Gephyrocapsa huxleyi* and added the following reference :

Bendif, E. M., Probert, I., Archontikis, O. A., Young, J. R., Beaufort, L., Rickaby, R. E., & Filatov, D. (2023). Rapid diversification underlying the global dominance of a cosmopolitan phytoplankton. *The ISME Journal*, 17, 630–640.

We also modified the introduction to improve precision and added the appropriate reference:

“As photosynthetic organisms, coccolithophores contribute 1-10% to global ocean primary production (Poulton et al., 2007) and about 50% to the deep ocean flux of particulate inorganic carbon (PIC; Neukermans et al., 2023).”

Line 36 & 37 & 60 : cocco or Ehux ? Throughout the manuscript the authors use one or the other interchangeably. Please stick to one wording consistently.

Within the group of coccolithophores, *G. huxleyi* is the only coccolithophore species that is known to form blooms at temperate to high latitudes. Therefore, in our study, the terms “coccolithophore blooms” and “*G. huxleyi* blooms” can be used interchangeably. We however agree with the reviewer that this can be confusing and have therefore decided to stick to “*G. huxleyi* blooms”.

Line 69: space (and coma?) missing: “(Guinaldo et al., 2025)on top”

Done

Line 72-81: I am a bit puzzled by this paragraph and the use of the term “climate variability” although I see what the authors mean as they refer to Sando et al. 2010. However, the authors of this study in 2010, made sure to re-define this term as they used a pretty narrow definition where climate is limited to ocean heat transport. In ocean modelling, we use climate for atmospheric conditions/forcings for instance. It seems that the authors here are making the confusion (or just are not being specific enough in the wording, maybe replace “climate variability” by precisely what you actually mean OR define it) between atmospheric conditions, climate variability and ocean heat transport. It seems that the authors are trying to explain that warming in winter is a remote effect (through advection – ocean heat flux) whereas in summer, it’s a local effect (local atmospheric warming). Could you re-phrase this paragraph?

We were mentioning climate variability at various timescale, e.g. multi-decennial variability related to the AMV, interannual variability related to the atmospheric conditions/weather regimes. However, we agree that our mention of “climate variability” is indeed confusing. Therefore, in the revised version, we decided to modify these lines.

Sentence modified :

“Even at the northern edge of the North Atlantic, the BS atmospheric and oceanic internal variability responds to NAO conditions (Levitus et al., 2009; Chafik et al., 2015), while 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.”

Line 84: thermal range of coccos, which is ? there is a tendency to build sentences like this one with “while” in middle connection two informations which are not related, quite confusing to read and energy-demanding to reconstruct. Maybe you mean something like :

“ In the CS, oceanic conditions remained favorable for coccolithophores until mid-June ... while ... the second half of summer was marked by less favorable conditions. ”

Furthermore, I do not understand how temperatures exceeding upper thermal range can be a favourable condition for growth. If I try to the brain gym, I go in the first paragraph (or Fig. 2b) and I infer SST is about 17.5degC in the CS. What is the upper thermal range definition ? It is not define unless I missed the obvious. Help the reader, repeat numbers, define concepts, and repeat references to figures (Fig. 2a,b), etc.

We agree that there is a lack of detail regarding the temperature range and other specific aspects of the phenology of *G. Huxleyi*. In the revised version, we have included references supporting this temperature range and details in the main text and in the section on methods.

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) (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, 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 (2015), based on a global compilation of in situ measurements of coccolithophore species abundance and diversity (O’Brien et al., 2013)”

Methods section :

“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 (O’Brien, 2015)”

Lines 99: “The primary limiting factor for blooms in the BS is the photosynthetically active radiation (PAR), which drives bloom onset and decline.”

That is a bold statement without any reference. Maybe true in general, but we know that *Ehux* occupy a niche that is not only driven by light. It is for example shown that viral lysis can terminate such blooms. Plus, this is interpretation because your findings do not back up this result.

Additionally, you start the paragraph with “The PIC dynamics reflected these environmental conditions” and finishes with “This bloom dynamic correlated with the environmental

Conditions” . vague statement, never quantitative or specific. No description of environmental description is given in this paragraph so the reader has to remind perfectly the previous section. Painful. Try to be specific, the earlier the better. What bloom dynamic (peak? Bloom duration?)

To account for both the comment of Rev#1 and Rev#2 the section 2.1 has been revised accordingly with the inclusion of a specific paragraph dedicated to PAR analysis and atmospheric conditions.

“Likewise, PAR in CS was strong in May-June with values surpassing 42 Einstein.m⁻².day⁻¹ (upper-range of the optimal conditions for *G.huxleyi* with thresholds established from the study of the species’ realized ecological niche; see Sect.A1.4 and O’Brien (2015)) with conditions becoming more favorable in July onward (Fig.2c). These variations are primarily influenced by the atmospheric conditions, specifically cloud cover. In June, a persistent high-pressure system over Fennoscandia (Fig.A1) led to exceptionally weak wind conditions (Fig.A2) and low cloud cover (Fig.A3) but increased toward climatological values onward . In BS, PAR was exceptionally high compared to the summer climatology allowing sufficient sunlight to reach the surface ocean for photosynthesis throughout summer (Fig.2d). These results are influenced by the cloud cover over BS where a large portion of the sea experienced significant clear-sky conditions during summer (Fig.A3)”

We also added figures to analyse the environmental conditions (Fig A1, A2 & A3) and the PAR evolution in 2023 (Fig 2 c-d).

Figure 1. Ocean-atmosphere conditions in June-July-August-September 2023. Standardised monthly anomalies from ERA5 in 2023 compared to the 1991-2020 climatological period for mean sea level pressure

Figure A2. Same as Fig.A1 for 10-m wind speed

Figure A3. Same as Fig.A1 for total cloud cover

Figure 2. Daily spatially averaged SST, MLD and PAR variables for 2023. Spatially averaged SST (black solid line) and MLD (blue solid line) anomalies for 2023 in (a) the Celtic Sea and (b) the Barents Sea. The black dashed line represents the climatological SST averaged over each basin for the period 1991–2020, while the green dashed line marks the 90th percentile threshold for MHWs, as defined by (Hobday et al., 2016). Red shading indicates periods of MHWs, while grey shading highlights conditions favorable to *G.Huxleyi* blooms based on optimal ranges for SST and MLD in the species' realized ecological niche (see Sect.A1.4; O'Brien, 2015). Spatially averaged PAR for 2023 in (c) the Celtic Sea and (d) the Barents Sea. The vertical brown lines inform on the optimal range for *G.Huxleyi* blooms (see Sect.A1.4)

Line 102: “potentially reflecting the multi-annual North Atlantic variability...”

Another interpretation that should go in the discussion and that is not supported by results here. Speculation.

This sentence and the related notion are not a result. We have decided to remove it.

Line 109: “linked to increased atlantification” where /how do you document Atlantification ? By the position of the polar front ? Say it here. This article is for experts only. You say it later lines 115-116.

We agree on the lack of detail regarding the position of the polar front and its consequences on PIC distribution. We have added two figures (A7 and A8) and relevant references to support our findings.

Figure A7. Shifting position of the polar front in the Barents Sea. (a) Position of the polar front in the Barents Sea obtained from remotely sensed SST imagery and (b) corresponding position of the polar front maximum latitude in the western (blue lines) and eastern (orange lines) basins of the Barents Sea over the period 1998-2023.

Figure A8. Shifting position of the leading edge of *G. huxleyi* summer blooms in the Barents Sea. Temporal evolution of the mean latitude of the bloom summer maximum extent for the western (blue lines) and eastern (orange lines) basins of the Barents Sea over the period 1998-2023.

Line 116: “Interannual variability in the position of the polar front is accompanied by shifts in PIC maxima,” another vague and non-demonstrated statement. Is there a cause-consequence demonstration that the position of the polar front influence PIC max ? I don’t see it at least.

References are provided in the study to demonstrate this point (Oziel et al. 2020, Neukermans et al 2018). We’ve also added Fig A7 (see comment above) about the polar front shifting position and corresponding shifting position of PIC max (Fig A8, see comment above) with also a mention in the Results section.

Line 122: First reference of methods here as section A1. Which should actually be A1.3. If you want to use methods as supplementary, you need to be irreproachable. You are not. References to other methods sections are not proper. All methods should be cited like here in order: study cite when you first introduce BS and CS, Satellite data. No MHV definition. Btw, MLD is no satellite data.

We agree with the reviewer that our references to methodological sections lacked accuracy. . We have carefully checked the entire manuscript on these aspects (order of the methods and their referencing) and corrected where necessary.

Line 145: double bracket ((. The studied area is the Arctic ? I thought it was the North Atlantic? Barents Sea could be both as a frontal area but you need, again, to be consistent. Sea-ice melt induced stratification does not “facilitate the accumulation of nutrients”. It just stratifies. And then “These processes likely contributed to the unprecedented bloom intensities observed in recent years.” ... A purely speculative paragraph in the result sections...

We agree on the speculative nature of the paragraph and have removed it, as we did for the sentence on sea-ice melt and stratification.

Line 152: “Here, the bloom period remains limited by PAR availability” Where is the demonstration ??? Are we doing science here ?

Our revised analyses now include observational evidence on PAR availability (Figure 2 c and d, see comment above).

Line 157: So now “The establishment of these temperatures was locally modulated by climate variability” so what is meant here ? Climate variability is ocean heat transport or atmospheric warming. If the former, it’s not local, it’s remote. If you mean atmospheric warming, then you have revise entirely the introduction and better frame/define.

In this paragraph, we addressed variability at different timescales and its impact on SSTs. This sentence refers to the amplification of the 2023 MHW event by shorter-scale atmospheric variability and multidecadal variability (AMV) and the related reference. Recognizing that this sentence was not necessary in the context of this study, we decided to delete it.

Line 160: Coccos or E. Huxleyi ?

In line with a previous comment about consistency, we decided to stick to *G. huxleyi*.

Line 161: Another new un-defined term: “optimal bloom development zones”

We acknowledge that we used different terms for the same concept. We therefore checked for consistency throughout the document. This term was part of a sentence that was deleted in the revised version.

Line 162: “in trailing/leading regions” not defined or referenced to methods. The authors are asking the readers to read their mind. Definition in methods is incomplete.

Trailing and leading edge are now defined and associated with references in the Methods and the main text.

Main text :

“the Celtic Sea and the Barents Sea, respectively representing the trailing (or equatorward) edge and the leading (or poleward) edge of *G. huxleyi* bloom distribution in the North Atlantic Ocean (Winter et al. 2014)”

Methods :

“In the North Atlantic, *G. huxleyi* typically blooms annually in regions situated between the continental shelf of Western Europe (Celtic Sea) and an Arctic shelf Sea (Barents Sea), respectively representing the trailing and leading edges of the bloom distribution (Winter et al, 2014, Neukermans et al, 2018)”

Line 164: Okay, but you do not investigate any ocean currents... am I right ? Why ?

Yes, the reviewer is right that ocean currents were not specifically investigated - the polar front position was. Therefore, we have removed this statement.

Line 166: Impact the surface area ? What does that mean ? it changes the surface area of the Barents Sea ?

We acknowledge that this sentence lacks clarity. We have revised the conclusions section entirely, which no longer includes this statement.

Line 175: and the fact that coccolith sheds light when they shed, i.e. when the bloom is dying...

It is unclear to us what this comment refers to.

Line 176: or modelling them?

This study intentionally focuses on an observational analysis of the impact of MHW on PIC. We fully understand the need for modeling to disentangle the various factors and quantify the extent to which each contributes to blooms, but we consider this to be beyond the scope of our study.

Line 178: Now another concept: ecological niche. First time. Not defined, not characterized.

Details added in the Methods section:

“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 et al 2015).”

Line 180-182: Did I see an analysis on atmospheric winds ? Storms ? Air temperature ? PAR?

We agree that this is a major weakness. We have added figures A1, A2 & A3 showing atmospheric conditions from May to September and the temporal evolution of PAR in both regions.

Line 190 : This lesson is hard to take by a study which does not produce any data or study any process.

Rephrased as follows:

“This effort could be developed by considering a combination of multi-scale observation networks capable of providing the initial conditions, and enhanced modelling frameworks that capture subsurface dynamics and multistressor interactions to anticipate future changes and inform adaptive strategies for marine ecosystems (Gregg and Casey, 2007; Nissen et al., 2018; Krumhardt et al., 2019).”

Line 195: “This study reaffirms the poleward expansion of temperate phytoplankton communities” This is a lie ... where is documented this poleward expansion ? You did not bring any analysis that support that or add to the previous literature. Same for “highlights the emergence of new ecological hotspots in high-latitude regions”. Words mean something. Have you conducted a time-of-emergence analysis ? How did you show an emergence ? How do you support it ?

This section has been completely revised to meet both Rev#1 and #Rev2 comment. Specifically, we have added an analysis of the shifting polar front position (Figure A7, see comment above) in the revised manuscript) demonstrating the poleward expansion of *G. huxleyi* blooms.

Line 198: “These shifts, while globally evident, impact regional biogeochemical cycles and food web dynamics.” I do not understand the sense of this sentence, what is evident at global scale ? And How does this oppose regional bgc cycles and food web dynamics.

This section has been completely revised to meet both Rev#1 and #Rev2 comment.

Line 199: “Predatory species” ... un-related. Coccos are not an important food source, neither a big share of the phyto biomass.

It has indeed long been thought that coccolithophores are not an important food source for zooplankton. However, recent work by Dean et al. (2024 <https://www.science.org/doi/10.1126/sciadv.adr5453>) or Meyers et al. (2020, <https://doi.org/10.1016/j.pocean.2018.02.024>) shows that microzooplankton can exert strong top-down control on both bloom and non-bloom coccolithophore populations, grazing over 60% of daily growth. Furthermore, microzooplankton grazing is now considered a major driver of the dissolution of calcite in shallow waters (e.g., Dear et al. 2024, Ziveri et al. 2023; <https://www.nature.com/articles/s41467-023-36177-w>)

Line 204: No reference for arctic acidification ? Really.

The reference was not displayed in the first version. Corrections made.

Line 207 : It is not counter-intuitive, sea-ice is melting away (even in winter) and there is more ocean-atm interactions/forcing. Plus there is a compensation effect with the outflowing freshwaters in the Fram strait. So this is both a buoyancy and mechanical effect.

Sentence removed as it is beyond the scope of the study.

Line 209: wrong placement of citation. Sallée et al. 2021 is about MLD and stratification ONLY.

Correction made.

“These dynamics, including the vertical variation of the summertime mixed-layer depth (Sallée et al., 2021), may reduce both light and nutrient availability, and also have implications for carbon export, a critical function of calcifying species”

Line 209: speculations again and again. How is that calcifying species is a critical carbon sequester ? I though calcification produces CO₂ ? I am teasing because you just through out concept without explaining anything. The carbonate pump of course is responsible for a small share of the BCP. But why this is important them ? Through What process ? What is sequestration ? Do you define it ? it's not trivial at all.

Coccolithophores play a complex role in the carbon cycle as on the one hand their calcification produces CO₂, but on the other hand, their dense calcite scales are thought to enhance the sinking of organic matter to the deep ocean through the so-called ballast effect of aggregates. This has been a topic of debate for over two decades (as discussed in detail in Neukermans et al. 2023, Earth Science Reviews).

This dual role has been referred to in the introduction and has been reiterated only very briefly in the conclusion section as follows: “Additionally, the evolution of water column stratification plays a key role in promoting blooms with a clear signal in the North Atlantic which in fine may alter the regional carbon cycle.”

Line 212: “the Barents Sea’s historical increases in bloom intensity may reflect enhanced nutrient inputs, favorable light conditions, and prolonged ice-free seasons driven by Arctic warming.” Coccos do not need much nutrients, check literature. Are coccos in the Arctic Waters ? I though they were staying south of the polar front. What connection with sea-ice then ? For the BS, how can you discard grazing pressure ? Viral lysis ? other losses ? Which driver is more important ? How do you choose what is important ? Also for CS, I mean, is there less light in the CS ? Less nutrients? Do you provide support for any claim ?

This section has been completely revised to address comments Rev#1 and #Rev2. In the new Conclusion section we have removed the sentence.

Line 215: “Tipping point” It feels like the authors need to name drop every fancy concepts.

We acknowledge the sentence does not provide enough information to discuss the results and we have decided to remove it.

Line 216: First appearance of modelling...

While designing the study we made the choice to rely on satellite observations and describe the consequences of MHW. We acknowledge this may introduce biases but are convinced about the potential of observations only to evaluate the impacts.

Line 242: trailing edge / leading edge of what ? the blooms or the North Atlantic... ?

As mentioned before, we added details on trailing and leading edge of bloom distribution.

“In the North Atlantic, *G. huxleyi* typically bloom annually in regions situated between the continental shelf of Western Europe (Celtic Sea) and an Arctic shelf Sea (Barents Sea), respectively representing the trailing and leading edges of the bloom distribution (Winter et al, 2014, Neukermans et al, 2018)”

Line 245: provide ETOPO version.

Version added : “The bathymetric limits are respectively -150 m and -100 m for the Celtic Sea and the Barents Sea and derived from the ETOPO 2022 global relief model at 60 arc-second resolution (MacFerrin et al., 2024)”

Line 278: Ah ! So the upper thermal range is here, and is 16degC ? How those criterions have been decided ? Is it arbitrary ?

References added to explain how these ranges have been decided.

“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 et al 2015).”