

Review of “Hysteresis of phytoplankton communities over Subpolar North Atlantic to CO₂ forcing” by Lee et al.

'Comment on egusphere-2025-1474' | Anonymous Referee #1:

Review

This manuscript analyses climate model results of phytoplankton response in the North Atlantic. It examines a scenario of so-called “negative emissions” which implies artificial removal of CO₂ from the atmosphere. The authors focus on differences between a future time (around year 2200) at which CO₂ concentrations are back levels of ~400 ppm corresponding to approximately the year 2000 after having peaked at more than 700 ppm around year 2100. They find large differences in phytoplankton composition between those time periods, despite similar levels of CO₂, and term this phenomenon “hysteresis”. The manuscript is well written and nicely illustrated and would be interesting for readers of this journal.

Response : We thank the referee for encouraging and insightful comments. We have carefully addressed all comments and revised the manuscript accordingly by fully incorporating the referee's suggestions.

Major Comments

I have two more major comments and a few minor technical suggestions. The first major comment concerns the use of the word “hysteresis” in the title and elsewhere in the manuscript. It is different from the original use in physics (electrodynamics), where it describes differences in EQUILIBRIUM states of a system for identical boundary conditions, where the differences arise only from the history of the system. It often implies thresholds that mark switching between those different states. Here, however, the system under consideration is not at equilibrium and the differences between the states are due to delays in the response. I think the use of this term (hysteresis) is not warranted in this context and suggest describing it using a different term. At least, a discussion is warranted of this issue.

Response: We thank you for your valuable comments. To avoid confusion for readers, we have replaced the term “hysteresis” with “irreversible shift” or “irreversible change” throughout the manuscript. Additionally, we have revised the title to “Irreversible phytoplankton community shifts over the subpolar North Atlantic to CO₂ forcing.”

The second major comment concerns the use of half-saturation coefficients to model nutrient uptake in their model. It would be good if the authors could clarify if the use constant half-saturation coefficients or variable ones. In the real ocean there is a variety of half-saturation coefficients depending on species and other factors and it has been argued that half-saturation values should be modeled as variable (Aumont et al. 2015). What would be the effects on the results if variable half-saturation coefficients were used, if MARBL uses constant ones?

Response: As the referee pointed out, in the real ocean phytoplankton half-saturation coefficients (K) vary across the phytoplankton functional types (PFTs). In CESM2's MARBL biogeochemistry model, each PFT is indeed assigned different half-saturation coefficients for each nutrient; however, these are prescribed as constant over time.

Following the referee's suggestion, we implemented the variable K approach of Aumont et al (2015) in which the effective K increases with PFT biomass and therefore varies in time as biomass changes. Specifically, we used the formulation:

$$P_1 = \min(PFT \text{ biomass}, P_{max}) \quad (1)$$

$$P_2 = \max(0, PFT \text{ biomass} - P_{max}) \quad (2)$$

$$K_{variable} = K_{constant} \times \frac{P_1 + sP_{rat} \times P_2}{P_1 + P_2} \quad (3)$$

Here, P_{max} is set as 1 mmol C m^{-3} and $sP_{rat} = 3$, where sP_{rat} represents how much larger the half-saturation constant K is for the large size class relative to the small size class within the same PFT (Aumont et al., 2015). In other words, in line with the remarks of Aumont et al (2015), which emphasize that an increase in phytoplankton biomass is typically associated with a larger phytoplankton class, we applied a variable half-saturation coefficient under high biomass conditions. Using this approach, we reproduced nutrient limitations for diatom and small phytoplankton. Consistent with the constant-K case, we found that the temporal evolution of nutrient limitation remains qualitatively similar (**Fig. R1**). For example, although there is a slight time difference, diatom nutrient limitation shifts from Si to N during the negative emission period and reverts during the Restoring period, while small phytoplankton are predominantly N-limited with only brief iron limitation at the beginning. Thus, the results are consistent regardless of whether constant or variable half-saturation coefficients.

Following the referee's suggestion, we explicitly stated in the manuscript that constant half-saturation coefficients are used in MARBL as below:

(163-166): Within MARBL—the biogeochemical component of the CESM2 Earth System Model—the advantage of smaller phytoplankton in low-nutrient environments is represented by prescribing different constant half-saturation coefficients for each PFT, reflecting the observed differences among phytoplankton size classes in the real ocean.

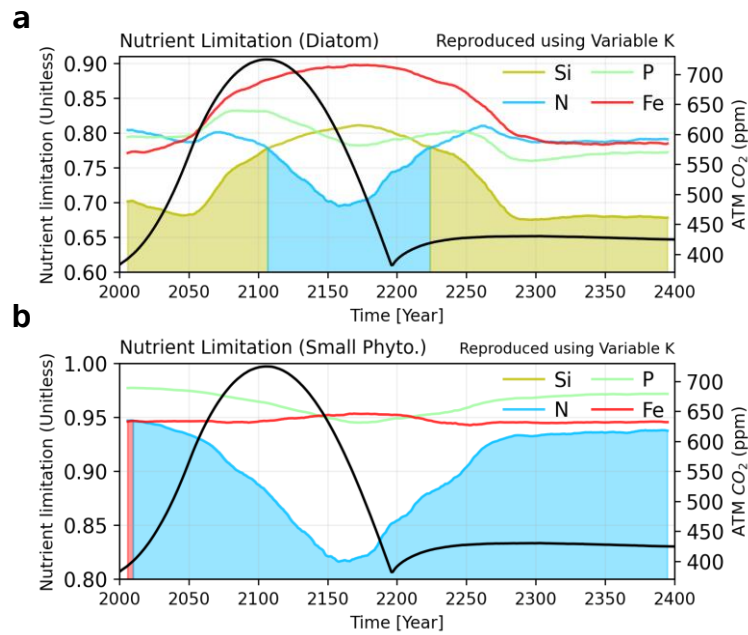


Figure R1. Nutrient limitation of **a**, diatom and **b**, small phytoplankton for four nutrients (SiO₃; dark-khaki, Nitrogen (N); blue, Phosphorus (P); light-green, Iron (Fe); red). All plots are drawn in 11-year moving averages and the shading indicates the primary limiting nutrients for each phytoplankton functional types.

Line by line comments

Line 166: "... *thereby promoting the growth of small phytoplankton.*" I think this would also apply to diatoms, right? If so, remove "small".

Response: Corrected.

84: "SO" explain acronym

Response: Corrected.

93: replace "Leibig" with "Liebig"

Response: Corrected.

96: Long reference is repeated.

Response: Corrected.

180: "(NO₃, SiO₃)" What about PO₄? Is it also decreasing? Is it modeled separately? I assume it could affect diazotrophs, who may be P limited.

Response: Both during the CO₂ increasing & decreasing period, surface PO₄ concentrations decrease continuously across the entire SPNA region and begin to recover shortly before the end of the negative-emission phase, similar to changes in NO₃ (**Fig R2**). Therefore, this result is consistent with the changes in P limitation values for both diatom and small phytoplankton shown in Fig. 3b and Fig. S5. As the referee mentioned, this PO₄ decline can affect diazotroph growth, which is not affected by N and Si, with sustained surface cooling due to the weakening of the AMOC strength.

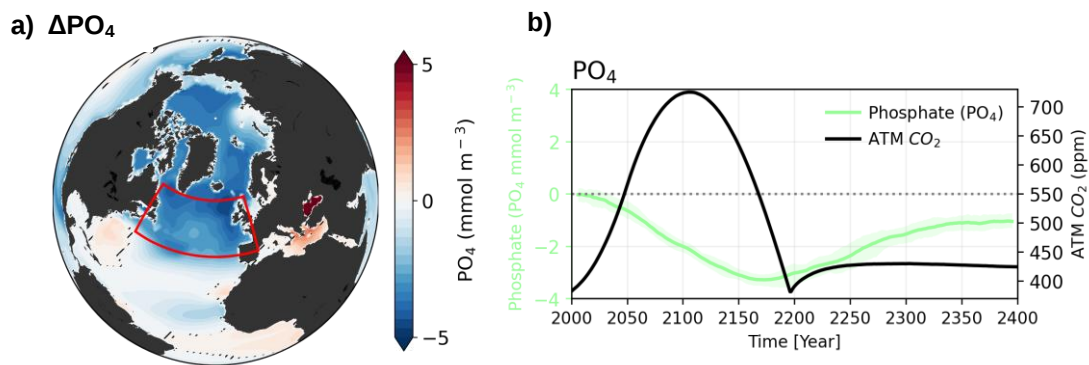


Figure R2. **a**, Difference in Phosphate (PO_4) between CO_2 down and climatology periods. **b**, Time series of changes in PO_4 (light-green) and atmospheric CO_2 concentration (black) compared to initial level (2001-year). The plot is drawn in 11-year moving averages and the shading indicates the minimum-maximum values between total ensembles.

186: “reported” by whom?

Response: Corrected.

208-209: but in SPNA it shifts from Fe limitation to N-limitation

Response: In the time-series (Fig. S5a), we show how the mean limitation values for each nutrient—averaged over the whole SPNA region. In contrast, the spatial maps (Figs. S5b-c) highlight the nutrient with the lowest values at each grid point as the nutrient limitation for that grid, indicating that iron (Fe) limitation may be more widespread in the SPNA region. However, when limitation values are averaged across SPNA region, N limitation dominant from the present climate period through the entire experimental period.

243-246, 274: the SPNA is a relatively small region of the global ocean. How much does global EP decrease and what is the contribution of the SPNA to it?

250-251: related to previous comment. This effect may not be large enough to affect atmospheric CO_2 significantly.

Response: Although the SPNA region covers only a relatively small area of the global ocean, it represents one of the most efficient regional biological carbon pump (Falkowski et al., 1998). During the Climatology period, the its area-averaged POC export flux is ~1.5 times higher the global mean. Quantitatively, although the SPNA occupies <2% of the global ocean area, SPNA region ($1.29 \times 10^{16} \text{ mmol C yr}^{-1}$) contributes $2.87 \pm 0.04\%$ of the global ocean ($4.49 \times 10^{17} \text{ mmol C yr}^{-1}$) POC export flux. In addition, strong AMOC-driven deep convection in this region enhances the downward transport and sequestration of organic carbon into the deep ocean, so despite its limited spatial extent the SPNA exerts a great contribution to global export production and long-term carbon sequestration.

Additionally, the irreversible shift toward smaller phytoplankton in the SPNA reduces the region's carbon sequestration capacity, which can locally intensify ocean acidification and thereby exert biological stress on calcifying organisms (e.g., coral reefs). Beyond its biogeochemical implications, such changes in phytoplankton community structure can also affect regional fisheries, with cascading socio-economic affects for neighboring countries.

259-260: Not sure this is the whole reason, since diazotrophs also decrease in the subtropical North Atlantic where SSTs do not decrease.

Response: The strong decline of diazotrophs is primarily driven by temperature limitation in the SPNA region because diazotrophs cannot survive at temperatures below ~15°C (Long et al., 2021). Therefore, the persistent AMOC-driven SST cooling reduces the extent of habitable region above this threshold. This explains the substantial decline in diazotrophs across the SPNA. In addition, suppressed nutrient availability can decline the diazotroph concentrations as well.

In contrast, the subtropical North Atlantic remains sufficiently warm that temperature is not a limiting factor. In this region, diazotrophs are instead regulated by nutrient availability. Unlike other phytoplankton groups, diazotrophs are not limited by nitrate (NO_3) or silicate (SiO_3); rather, they are affected by phosphate (PO_4) and iron (Fe) supply.

To avoid confusion for readers, we have clarified in the revised text that, in addition to temperature limitation, the role of suppressed nutrient availability as a secondary factor has also been stated.

(263-265): The diazotroph concentrations significantly decrease, primarily reflecting the response to oceanic temperature changes, while suppressed nutrient availability contributes as well

268: why is nutrient recovery delayed?

Response: Previous studies have suggested that global warming leads to a weakening of the nutrient cycle, particularly through enhanced Southern Ocean (SO) productivity that intensifies nutrient trapping in the deep ocean and drives a global nutrient decline (Moore et al., 2018; Laufkötter and Gruber, 2018). Such large-scale nutrient redistribution is sustained even under the negative emissions (**Fig. R3**). Therefore, it implies that even when the AMOC begins to recover during the CO₂ decreasing period, the amount of nutrients supplied from the Southern Hemisphere and lower latitudes remains reduced compared to the climatology period.

In addition, during the weakened AMOC phase, the mixed layer depth (MLD) in the SPNA region remains in a shutdown state, and its recovery requires sufficient salt-advection associated with AMOC strengthening (Oh et al., 2022). Therefore, the MLD can begin to recover after the salt-advection has sufficiently accumulated. As a result, the recovered nutrient levels stay below the climatological state, giving rise to the delayed recovery.

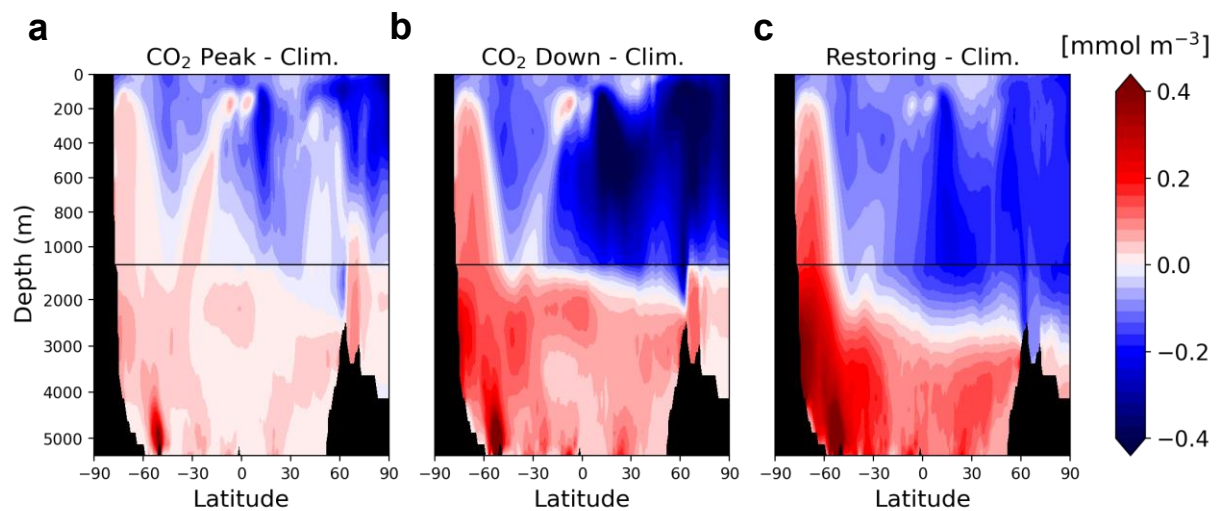


Figure R3. Zonally averaged differences in the vertical profile of dissolved inorganic phosphate (PO₄) between the Climatology and **a**, CO₂ peak, **b**, CO₂ Down, and **c**, Restoring period.

273-274: should it be “positive” rather than “negative” feedback?

Response: Corrected.

281-283: It may be worthwhile to note here that the GFDL model does not exhibit "hysteresis"

Response: While it is true that diatom concentrations almost return to their initial values after CO₂ is decreased to the initial level, our analysis indicates that the pathway during the CO₂ Ramp-down period does not follow the same pathway as the CO₂ Ramp-up period, indicating the hysteresis.

This is evident in the scatter plot, plotting diatom concentrations directly against atmospheric CO₂ (**Fig. R4**), which shows a clear separation between the Ramp-up and Ramp-down periods. Therefore, we interpret this as evidence of a hysteresis response in the GFDL-ESM4 model, even though the end state after CO₂ recovery appears close to the initial state.

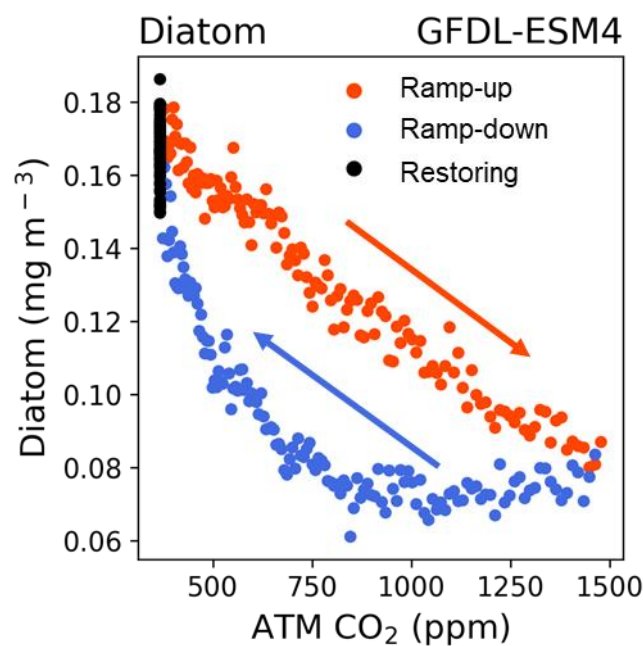


Figure R4. Changes in SPNA area-averaged diatom concentrations (y-axis) corresponding to global mean atmospheric CO₂ concentration (x-axis). The colors in scatters indicate the 3 periods (CO₂ Ramp-up period; orange, CO₂ Ramp-down period; blue, Restoring; black).

Reference

- Aumont, O., Ethé, C., Tagliabue, A., Bopp, L., and Gehlen, M.: PISCES-v2: An ocean biogeochemical model for carbon and ecosystem studies, *Geosci. Model Dev.*, 8, 2465–2513, <https://doi.org/10.5194/gmd-8-2465-2015>, 2015.
- Falkowski, P. G., Barber, R. T., and Smetacek, V.: Biogeochemical controls and feedbacks on ocean primary production, *Science (80-.)*, 281, 200–206, <https://doi.org/10.1126/science.281.5374.200>, 1998.
- Keith Moore, J., Fu, W., Primeau, F., Britten, G. L., Lindsay, K., Long, M., Doney, S. C., Mahowald, N., Hoffman, F., and Randerson, J. T.: Sustained climate warming drives declining marine biological productivity, *Science (80-.)*, 359, 113–1143, <https://doi.org/10.1126/science.aao6379>, 2018.
- Laufkötter, C. and Gruber, N.: Will marine productivity wane?, *Science (80-.)*, 359, 1103–1104, <https://doi.org/10.1126/science.aat0795>, 2018.
- Long, M. C., Moore, J. K., Lindsay, K., Levy, M., Doney, S. C., Luo, J. Y., Krumhardt, K. M., Letscher, R. T., Grover, M., and Sylvester, Z. T.: Simulations With the Marine Biogeochemistry Library (MARBL), *J. Adv. Model. Earth Syst.*, 13, <https://doi.org/10.1029/2021MS002647>, 2021.
- Oh, J. H., An, S. Il, Shin, J., and Kug, J. S.: Centennial Memory of the Arctic Ocean for Future Arctic Climate Recovery in Response to a Carbon Dioxide Removal, *Earth's Futur.*, 10, <https://doi.org/10.1029/2022EF002804>, 2022.

RC2: 'Comment on egusphere-2025-1474', Rebecca Wright,

Summary

The authors present an interesting and generally well-written and well-structured manuscript investigating the response of phytoplankton communities to future climate change and “negative emissions” using model simulations. They find substantial shifts in community composition towards smaller species, which persist after atmospheric CO₂ concentrations are reduced. They attribute these shifts primarily to changes in the Atlantic Meridional Overturning Circulation (AMOC) and nutrient availability, and highlight the negative consequences for carbon export efficiency.

Response: We thank the reviewer for his/her encouraging and constructive comments on our manuscript. We have carefully considered all points raised and revised the manuscript to fully incorporate the reviewer’s valuable suggestions.

Overarching comments

I have some reservations about the use of “hysteresis” as the key term to describe the main findings. The term is likely unfamiliar to many readers and risks obscuring the central message, while also not being used entirely accurately in this context. Throughout the introduction, the authors refer to “irreversible responses”, “irreversible changes”, and state “we report irreversible shifts”, which sets the expectation that this language will underpin the key message of the paper. I therefore recommend replacing “hysteresis” with “irreversible shifts” or “irreversible changes” throughout the manuscript. Alternatively, if the authors wish to retain “hysteresis”, it should be clearly defined and introduced in the introduction rather than appearing for the first time, with no explanation, in the Experimental Design section (line 114).

Response: We thank the referee for the valuable comment. For easier readability for the reader, we have replaced the term “hysteresis” with “irreversible shift” or “irreversible change” throughout the manuscript. Additionally, we have revised the title to “Irreversible phytoplankton community shifts over the subpolar North Atlantic to CO₂ forcing.”

Line by line comments

84: The acronym SO is undefined at this point. At line 132 it is defined as Southern Ocean, but that seems inconsistent here given the study's focus on the SPNA region. Please clarify or correct.

Response: We have defined the acronym “SO” on line 84. Additionally, to keep the focus of the manuscript clear, we have removed descriptions about the Southern Ocean and omitted the Supplementary Figure 1 that presented the global map of the BC index.

96: Duplicated Long et al. (2021) reference.

Response: Corrected.

120-130: The description of the statistical method (“The statistical method ... [] ... simulation”) would fit better in the Methods section rather than the Results.

Response: We have displaced a methodological description of the Bray–Curtis (BC) dissimilarity method in the Methods section.

186: the statement ‘... it has been reported that...’ requires a reference.

Response: Corrected. We added related references.

244: ‘prestige’ seems inappropriate in this context; consider replacing it with ‘lose this status’.

Response: Corrected.

262: ‘negative CO2 emission’ should be changed to ‘negative CO2 emissions’.

Response: Corrected.

269-270: ‘exacerbated’ means to intensify or increase, which is the opposite of what you report in your results for carbon export. This word needs changing to ‘reduced’ or a suitable synonym.

Response: Corrected.

Figure 1: The green used for Diatoms in panel (b) is identical to the green used for Ramp-Up in panels (c–e), which could be confusing. I recommend selecting a different colour for the diatom category to avoid ambiguity.

Response: Corrected. We changed to different colors to avoid ambiguity.