

We would like to thank the reviewers for their time and patience in giving constructive criticism and suggestions to improve the manuscript. Their comments have helped us improve the clarity and scope of the manuscript. Our major results have not changed. In response to their recommendations, we have addressed all reviewer comments, incorporating their suggested modification, which include:

- Clarifying the scope of the model and to carefully constrain our interpretation of the results to what can be inferred from model simulations.
- Additional details on how air-sea CO₂ flux is calculated in the model
- An acknowledgement of our model's limitations, including on the absence of epibionts and coccolithophores which will reduce CDR efficiency even more.

For ease of reference, the line numbers in this response correspond to those in the tracked changes document. Reviewer's comments are presented in black, authors' responses are presented in blue, and the modification in the manuscript is written in italics.

Reviewer #1 Evaluations:

This paper develops a model to examine how macroalgae cultivation and harvesting affects mCDR efficacy and marine biogeochemistry. The paper examines three hypotheses, (1) the extent to which macroalgae cultivation can add to mCDR, (2) how nutrient uptake and light limitation affects lower trophic levels, and (3) the consequences of dumping macroalgae biomass on the biogeochemistry of deep ocean waters.

This investigation is done by combining information from NEMO and ERA5 and modifying MEDUSA and using parameters from the literature. A number of assumptions are made to model parameters.

The paper adequately addresses hypothesis (1) see Figure 3, where the authors show that total PgC /yr changes with model parameters. However, I am not convinced that the paper address (2); although the paper suggests that phytoplankton NPP was reduced by macroalgae, I think this is an over-interpretation of the model results. I am not convinced that slow-growing macroalgae will greatly affect phytoplankton NPP. The model shows that phytoplankton NPP is reduced by macroalgae, but this is after ignoring herbivory and trophic interactions.

We thank the reviewer for highlighting that several aspects of the manuscript could benefit from clearer framing regarding model scope and ecological realism. To address this, we revise hypothesis 2 (line 72 in the original manuscript) to (line 76-78 in the tracked changed document):

How does large-scale macroalgae cultivation modify nutrient and light availability, and what are the resulting biogeochemical responses of phytoplankton and the biological pump?

Regarding hypothesis (2), we agree with the reviewer that our original draft potentially overstates the strength of our conclusion regarding phytoplankton NPP. Our intention was to quantify the potential biogeochemical pressure exerted on phytoplankton by large-scale macroalgae cultivation through competition for nutrients and light at climate relevant spatial scales. To address this concern, we have revised text in the results and discussion to explicitly state that the reduction in NPP represents an upper-bound estimate of resource competition under the simplified trophic assumptions of the model. Specifically, we revise this statement of results from section 3.3 (line 280-283 in the original manuscript):

Large-scale macroalgae cultivation substantially altered lower trophic levels by reducing nutrient availability and shading phytoplankton. In the default simulation, phytoplankton

NPP fell by 49.78% ($-24.81 \text{ Pg C yr}^{-1}$), accompanied by declines of 45.40% in phytoplankton biomass

... to ... (line 334-339 in the tracked change document)

Large-scale macroalgae cultivation substantially altered surface nutrient availability and light conditions, leading to pronounced changes in phytoplankton NPP. Note that these changes reflect competition for nutrients and light as represented in the model and provide an indicative estimate of the potential biogeochemical response, rather than a detailed prediction of realised ecosystem behaviour. In the default simulation NPP fell by 49.78% ($-24.81 \text{ Pg C yr}^{-1}$), accompanied by declines of phytoplankton (45.40%) and zooplankton (47.16%) biomass...

The non-harvesting loss includes implicit herbivory, and it is part of our sensitivity test (see table 2), and we have shown that increasing this parameter can decrease macroalgae NPP by ~5% but phytoplankton NPP is reduced less (-38.2% in high loss experiment, compared to -49.8% in default simulation, see Fig 3). To avoid ambiguity, we have added an explicit discussion of how macroalgal growth rates, grazing pressure / herbivory, and trophic interactions reduce or redistribute these impacts in real life. In the Discussion section we add the following text to better explain things (section 4.1 line 388-393 in the tracked change document):

... However it is also important to note that the macroalgae submodule includes only a simple loss term and does not explicitly resolve grazing or other higher trophic food-web feedbacks (e.g. in Wu et al., 2023, Wu et al., 2025 zooplankton grazing is explicitly represented). As a result, the simulated reduction in phytoplankton NPP and zooplankton biomass reported here may represent an overestimation, because explicit herbivory on macroalgae could recycle nutrients and reduce the impact on phytoplankton NPP, as illustrated from the high loss experiment (see Fig 3). This makes the simulated phytoplankton response in this study a first-order biogeochemical estimate of potential competition effects.

Finally, (3) there is little discussion regarding biogeochemical impacts and given the model, this hypotheses/section is not needed.

Regarding hypothesis (3), we would agree that our model is not designed to resolve detailed benthic ecological and biogeochemical responses. However, we have retained this analysis because the oxygen consumption and nutrient regeneration associated with large-scale biomass sinking still represents a fundamental biogeochemical effect that should be highlighted in mCDR studies. We have rewritten this statement in the abstract ...

Sinking of the harvested biomass to the deep ocean drives widespread oxygen depletion (-20% globally), creating new suboxic zones in deposition regions.

... as ... (lines 7-9 in the tracked manuscript)

Sinking of harvested biomass increases oxygen demand during remineralisation leading to widespread oxygen depletion and the emergence of suboxic conditions at the seafloor in deposition regions.

Furthermore, we now emphasise the relative simplicity of MEDUSA's benthic ecosystem in the discussion (section 4.1 lines 408-411):

... We note that these results are not a detailed characterisation of benthic ecosystem impacts. MEDUSA's representation is intentionally simple, and a full assessment of seafloor community responses, including benthic respiration dynamics and faunal impacts, would require dedicated benthic ecological models. However, these results may be used to identify large-scale signals and patterns that would motivate future benthic studies.

Nevertheless, the paper is well written and logically structured, however the authors need to explore the literature regarding seaweed cultivation, especially with regards to differences between cold-water and warm-water species.

We thank the reviewer for the positive comments and their suggestion in exploring the difference between cold-water and warm-water species. We have added this in the method section (lines 154 - 157 in the tracked change document):

(Sargassum and Euchema). These taxa span a broad range of thermal niches and cultivation context: cold water species usually occupy high latitude, nutrient-rich upwelling systems, commonly found in North Atlantic aquaculture industry (Veenhof et al., 2024), while warm water species are predominantly cultivated in tropical and subtropical regions (Hayashi et al., 2017, Magcanta-Mortos et al., 2025).

And in the discussion (lines 488-496 in the tracked change document):

... The absence of riverine nutrient inputs and coastal-shelf processes also prevents realistic simulation of Sargassum dynamics (Wang et al., 2019) and likely underestimates the productive potential of warm-water cultivation in regions such as Southeast and East Asia where terrestrial nutrient subsidies support high macroalgal biomass in nearshore systems. Although the four taxa represented in this study span a range of thermal niches, cold and warm water taxa are associated with different cultivation systems, whereby warm water species are usually farmed using single step methods through vegetative propagation and low-cost fixed or floating raft systems in nearshore environments (Behera et al., 2022) while cold water species require multi-step propagation from spores, hatchery-based seeding, and deployment on longlines system (Boderskov et al., 2023; Bak et al., 2020). These differences are not captured in this idealised framework and mean that the modelled growth potential presented here translates differently to real-world aquaculture output depending on the region in question.

Some specific comments:

31-34 Provide some citations that support the concept that POC and DOC are released from macroalgae

Thank you for your suggestion, we have amended the manuscript to (line 32-34 in the tracked change document):

In natural systems, a substantial fraction of macroalgal NPP is lost as either particulate and dissolved organic carbon (POC and DOC), as demonstrated by experimental and field-based estimates (Kennedy and Blain, 2025; Chen et al., 2020) which may either be....

34-37 If macroalgae release POC and DOC as a fraction of NPP, then cultivated macroalgae can also be expected to release POC and DOC during production. I agree that harvest will remove most of the OC, however simply stating that no macroalgae carbon would be sequestered opposed the statement made in the previous statement.

We agree that cultivated macroalgae also release DOC and POC as a fraction of production, and we have revised the text to avoid the impression that sequestration is absent (line 38-40 in the tracked change document):

... after it reaches a target biomass (Arzeno-Soltero et al., 2023). While cultivated macroalgae release DOC and POC during growth, the removal of standing biomass during harvest limits the macroalgal-sequestered carbon, that can be exported to the deep ocean

and therefore limiting the potential contribution to climate-relevant carbon sequestration (Hurd et al., 2023).

123 Why was depth set between 5 to 10 m? In East Asia, species such as *Undaria pinnatifida* are cultivated on ropes deployed at depths of 1 m. Some types of *Saccharina* are also cultivated at 1 m depths. For some examples, see Choi et al. 2025. *Journal of Marine Science and Engineering* 13; Sato et al. 2023. *Frontiers in Marine Science* 10; Hwang et al. 2018. *Algae* 33

We agree that cultivation depth varies substantially depending on species, location, and farming practice. In this study we adopt a cultivation at 5 m following previous modelling study (Wu et al., 2023, 2025) and offshore cultivation experiment (Zollmann et al., 2023). This choice reflects a pragmatic modelling assumption intended to represent large-scale, offshore deployment, where deeper placement is often considered to reduce wave exposure and mechanical stress. The selected depth should not be interpreted as a prescription for optimal farming practice, nor as representative of nearshore cultivation systems. Rather, it provides a simplified representation of macroalgal biomass.

We have added citation for this sentence (original manuscript line 121 onwards, 140-144 in the tracked change document):

.... by default from approximately 5 to 30 m in the water column (10 model levels) following previous modelling studies (Wu et al., 2023, 2025) and offshore cultivation experiment (Zollmann et al., 2023). This depth range is intended to represent large-scale offshore cultivation and differs from nearshore farming practices, where shallower deployments are common (e.g. Choi et al., 2025; Sato et al., 2023, Hwang et al., 2018). We found negligible differences between cultivating macroalgae between 1-30m and 5-30m (results not shown).

130 *Macrocystis*, *Saccharina*, *Sargassum*, and *Eucheuma* all have different methods of cultivation. Note that *Sargassum* is not commonly cultivated and *Eucheuma* is cultivated in shallow waters.

We agree that *Macrocystis*, *Saccharina*, *Sargassum*, and *Eucheuma* are associated with different cultivation practices, and *Sargassum* is not commonly cultivated at present. Our intent is not to reproduce species-specific farming techniques or present-day cultivation practices. These taxa are used as a representative functional type, spanning a range of thermal niches and physiological traits, to explore the potential biogeochemical consequences of large-scale macroalgal cultivation. Therefore, we apply a common cultivation framework across taxa.

We added this sentence in the method section (2.2) line 161-163 in the tracked change document:

Although these taxa differ in their real-world cultivation methods and physiological traits, they are represented using a common idealised cultivation framework to isolate first-order biogeochemical effects at large spatial scales.

We also added that differences in cultivation protocols in the discussion are not covered in this study (see our response above)

Table 1

Growth rates of these four taxa are not the same; the same can be said for many of the parameters listed in this table. For example, even within taxa, the C content can vary between 0.2 to 0.4 mg / mg (Sato et al. 2025. *Phycological Research*).

We agree with the reviewer that the four taxa have different growth rates and other physiological parameters. We do not intend the values listed in Table 1 to represent taxon-specific physiological realism.

Instead, we adopt a common set of representative parameter values following Arzeno-Soltero et al. (2023), who has addressed this uncertainty explicitly by fitting and exploring parameter ranges

using a Monte Carlo framework. Our approach is consistent with this precedent and is intended to reduce model complexity while focusing on first-order, climate-relevant biogeochemical responses, and we have clarified this modelling choice in Table 1 caption in the revised manuscript:

We apply a common set of representative physiological parameters across macroalgal taxa in order to focus on first-order biogeochemical responses rather than species-specific physiological variability.

We also added some clarification in the method section (line 157-166)

All four are represented in identical functional form, with a number of shared parameters, but each species has different values for certain key parameters. These include optimal temperature range (between T^1_{opt} and T^2_{opt}), half-saturation constant for DIN uptake (k_{DIN}), and C:N ratio ($\Theta_{C:N}$) adopted from Arzeno-Soltero et al., (2023). Although the taxa considered here have different real-world cultivation methods, they are represented using a common, idealised cultivation framework to isolate first-order biogeochemical effects at large spatial scales. These, together with the shared parameters, are outlined in Table 1. We acknowledge that growth rates, carbon content, and other physiological traits vary considerably across and within taxa in reality (Sato et al., 2025), but rather reflects a functional representation designed to capture first-order biogeochemical effects at global scale. Our analysis therefore focuses on the sensitivity of large-scale biogeochemical responses to macroalgal cultivation.

What exactly is non-harvest loss? Is this the DOC and POC released during production? See Pain et al. 2021 Journal of Phycology 57; Canvin et al. 2024 Journal of Applied Phycology 36; Zhong et al. 2024 Marine Environmental Research 202; Neves et al. 2025 Science of the Total Environment 982;

In the context of our model, non-harvest loss represents all biomass losses that are not associated with harvest, including loss due to erosion, physical breakage, and implicit grazing. We would agree that in real macroalgal systems such losses can contribute to the release of both dissolved and particulate organic matter.

In the model, these losses are a function of biomass standing stock and not production per se, and in the default model we assume these are primarily associated with POC release so channel the losses to MEDUSA's slow-sinking detritus component (line 155 in the original manuscript). We accept that this simplification could be stated more clearly in the original manuscript, and have amended the reference in the method section from:

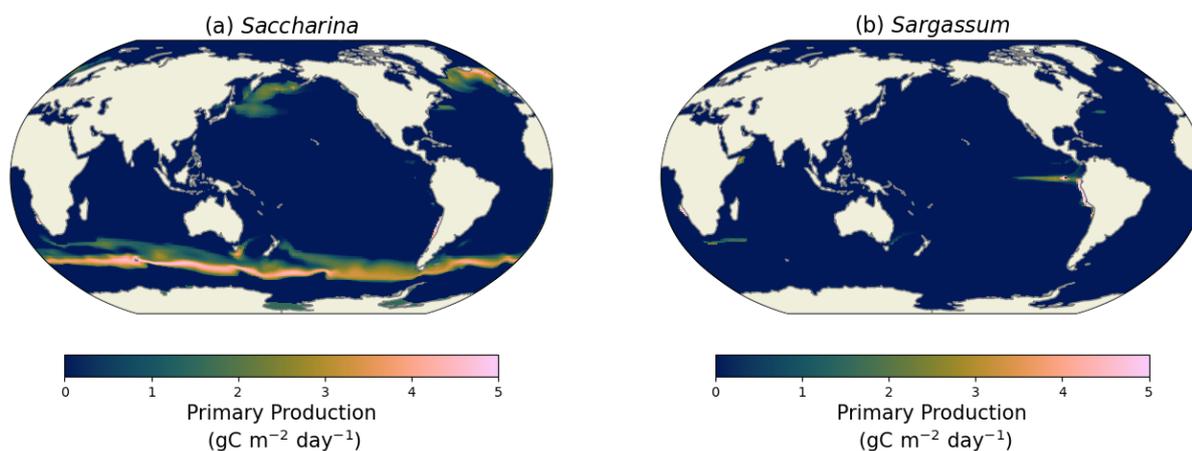
Macroalgae non-harvesting loss is modelled using a linear function, and is allocated to slow-sinking detritus

... to ... (lines 190-195)

In addition to harvesting, simulated macroalgae experience non-harvest losses, which represents biomass losses outside deliberate harvesting, such as physical erosion, aging, fragmentation, and implicit grazing processes. Non-harvesting loss are transferred directly to the slow detrital pool, where they are remineralised according to the standard MEDUSA slow sinking detritus formulation. As a result, processes such as direct DOC release during production are implicitly subsumed within the detrital pathway rather than treated explicitly.

Do the temperatures used in the simulation reflect the location where each taxa are expected to be cultivated?

Yes, we let the macroalgae grow everywhere in principle, but in practice the different taxa only grow within their temperature threshold, as described in equations 2-4. These equations describe a temperature dependent growth limitation that allows each macroalgal taxon to occupy its preferred thermal niche, such that cold-water species emerge at higher latitudes and warm-water species at lower latitudes, without prescribing explicit cultivation locations. Cold water species, such as saccharina, typically grow at high latitudes (>30 degrees N/S), while warm water species generally grow at lower latitudes. See Supplementary S1 below:



We have tried to make this clearer in the method section of the tracked change document (lines 176-178):

The temperature limitation term is similar to a Gaussian probability curve with flat peak, adopted from Arzeno-Soltero et al. (2023). ... The temperature limitation function acts as a smooth growth filter rather than a binary on-off switch. As such, growth declines gradually as temperature departs from the optimal range for each represented taxon, ensuring more realistic transitions across latitude and season.

Do the temperatures used in the simulation, which was run for 20 years, reflect the slow increase in water temperature and how this influenced the increase in herbivory due to herbivorous fish? See Verges et al. 2022 Scientific Reports 12; Barrientos et al. 2022 Frontiers in Marine Ecosystem Ecology 9

Yes for temperature– the model is realistic from the recent past (up to 2024), although over the relatively short period that we are simulating macroalgae growth the temperature change has been modest. We do not use any temperature dependency on non-harvest losses, such as herbivory. So, although the simulated macroalgae have experienced ocean warming, the effect of this in our simulations is limited. We have stated this in the method section of the revised manuscript (lines 127-129 in the tracked change document):

.. during the simulation until the end of the cycle. The temperature increase within this simulation period will be modest and therefore show limited effects on the macroalgae and other biogeochemical tracers.

When are the nutrients provided in the model? I assume it is a pulse, but the nutrient regime is not clear.

We thank the reviewer for noticing that we have not clarified the nutrient regime used in the model. Nutrients are not supplied as a pulse or external input. Macroalgae uses the ambient nutrients resolved by MEDUSA, therefore macroalgae are competing with phytoplankton for nutrients.

For the default simulation, and other experiments apart from iron-limitation sensitivity test, we exclude iron limitation. This should be interpreted as iron being supplemented or always at replete concentrations. We recognise that this was not sufficiently clear in the original manuscript and we have revised the text to explicitly state that macroalgal growth depends on ambient nutrient availability in the method section 2.2. (lines 146-148 in the tracked change document):

... and with its rate governed by temperature and the availability of light and ambient dissolved inorganic nitrogen (DIN) and iron (DFe). No external nutrient inputs or pulsed fertilisation are applied. As a result macroalgae compete directly with phytoplankton for the same nutrient resources.

And we also add clarification about iron supplementation by changing this sentence in the method (section 2.3, line 192-195 in the original manuscript):

However, in the default and other experiment except for Fe limitation, we assume that macroalgae is only limited by DIN while Fe is fertilised, following farming practices (Yamamoto et al., 2017), therefore when macroalgae is being remineralised ...

To (line 238-242 in the tracked changed document)

However, in the default simulation (as well as all other experiments except for Fe limitation), we assume that macroalgae are only limited by DIN. This corresponds to an assumption that Fe is supplemented, following established farming practices (Yamamoto et al., 2017), and that it is at non-limiting (replete) concentrations. When macroalgae is being remineralised ...

How is growth calculated? What is the initial biomass (inoculation) ?

We thank the reviewer for making us aware that these details have not been explained well in the manuscript. Macroalgal growth is calculated by applying a multiplicative formulation, in which biomass increases as a function of intrinsic growth rate which is modulated by temperature, light and nutrient limitation terms, similar to the formulation used for phytoplankton in MEDUSA.

Macroalgae cultivation is initiated using a small, non-zero initial biomass of $0.01 \text{ mmol N m}^{-3}$, consistent with the initial concentration used for other biological tracers in MEDUSA (e.g. phytoplankton, zooplankton, DIN).

We have added this information to the method section as below (line 134-137 in the tracked changed document):

We assume that macroalgae cultivation started from the last 20 years of the control run (2004-2023), starting from a small initial biomass of $0.01 \text{ mmol N m}^{-3}$. This initial value is consistent with other biological tracers in MEDUSA and serves as an “inoculation”, after which biomass grows in response to temperature, light and nutrient limitation.

221-223 “frequent harvest”: Generally, for most Saccharina species harvesting occurs during a set period of time and there is really only “one” harvest. For example, if a long-line of kelps are harvested, this can only occur once. Note that harvesting will only occur during the end of the cultivation season for most Saccharina and Sargassum species, such as *S. horneri* or *S. fusiforme*. In other words, harvesting is periodic and does not occur daily over the entire growing season.

In the manuscript, the harvesting does not occur daily; it only occurs when macroalgae reaches a certain threshold. From analysis of our model output, “frequent harvest” regions are those in which harvesting occurs on average three times a year.

3.1 Seaweed production and harvesting: This might be an ignorant question, but what happens to the unharvested seaweeds in the model? OR is all seaweed harvested?

We apologise for not making this clear in the manuscript. Unharvested seaweed will keep growing and will be harvested once it reached the threshold. We will make this clearer by amending this sentence in line 190-192 in the original manuscript in section 2.3:

To assess the sensitivity of target biomass in harvesting, we vary the harvesting thresholds to 200 and 800 mmol N m⁻². Since Fe ...

... To ... (lines 235-237 in the tracked changed document)

To assess the sensitivity of target biomass in harvesting, we vary the harvesting thresholds to 200 and 800 mmol N m⁻². Macroalgae are not harvested until they reach these target biomasses, so will continue to grow until they do (and will continue to experience non-harvest losses). Harvesting involves decreasing the biomass of macroalgae by 90% during the harvest day. Since Fe ...

230 Please provide details on how air-sea CO₂ flux is estimated.

Air-sea CO₂ flux is calculated using standard equations for the partition of dissolved inorganic carbon (DIC) into dissolved CO₂ (and carbonic acid), bicarbonate and carbonate ions. Partitioning is a function of local temperature, salinity, DIC and total alkalinity and uses the MOCSY submodel (Orr & Epitalon, 2015). The exchange of CO₂ uses the dissolved CO₂ fraction, in conjunction with atmospheric CO₂, temperature, salinity, and surface winds to calculate the exchange of CO₂ with the atmosphere, following the equations of Wanninkhof (2014).

We add a summary of how air-sea CO₂ flux is estimated in line 108-115 in the tracked changed document:

Air-sea CO₂ flux in NEMO-MEDUSA is calculated prognostically using standard equations for the partition of dissolved inorganic carbon (DIC) into dissolved CO₂ and carbonic acid, bicarbonate, and carbonate ions. Partitioning is a function of local temperature, salinity, DIC, and total alkalinity, and uses the MOCSY-2.0 carbonate chemistry routines (Orr and Epitalon, 2015). The exchange of CO₂ with the atmosphere is then calculated from the dissolved CO₂ fraction, atmospheric CO₂, temperature, salinity, and surface winds, following the gas transfer parameterisation of Wanninkhof (2014). Because gas transfer is finite and wind speed dependent, the rate at which surface ocean pCO₂ anomalies equilibrate with the atmosphere is limited, introducing a natural lag between biological carbon drawdown and atmospheric CO₂ uptake.

Figure 4 & 5 & 6 This is a very over-optimistic perspective of macroalgae cultivation. Why do the regions that have productive seaweed farms (i.e., East Asia, South East Asia) poorly resolved? Can we expect that seaweed cultivation can occur around Antarctica? These figures are a phytoplankton-centric perspective of seaweed cultivation.

We thank the reviewer for raising this important point regarding the apparent spatial patterns of macroalgae productivity shown in Figures 4-6. We agree that regions with well-established seaweed farming, especially in coastal East and Southeast Asia, are poorly resolved in our simulations. This limitation arises from the coarse spatial resolution of the global ocean model (please see revised text below) and the absence of key coastal processes such as riverine nutrient input and shelf sea dynamics, all of which are known to strongly influence macroalgae productivity.

Our simulations are therefore not intended to reproduce present-day coastal farming. Instead, they aim to explore the potential biogeochemical consequences of large-scale, offshore macroalgae

cultivation. In this context, regions such as the Southern Ocean emerge as highly productive in the model due to their persistently high DIN concentrations, consistent with previous global modelling studies (e.g. Arzeno-Soltero et al., 2023; Wu et al., 2023). We have acknowledged this in the revised Discussion that practical deployment of macroalgae cultivation in such regions would face substantial logistical and engineering challenges, which are beyond the scope of the present study: (line 467-470 in the tracked changed documents)

Although regions where high cumulative CO₂ share, CDR flux, and macroalgae NPP are located in the Southern Ocean, this area may not be suitable. Large-scale offshore macroalgae deployment would require extensive floating infrastructure, long-distance operations, and resilience to extreme wave and weather conditions (Jiao et al., 2025; Kwon et al., 2024). Such engineering and logistical considerations are not represented in the present model and remain outside the scope of this study.

Figures 4, 5, and 6 are presented in the context of ocean biogeochemical responses and therefore emphasise changes in nutrient distribution, NPP, and oxygen, rather than operational feasibility or spatial realism of seaweed farming. To emphasise this point, we have revised the text in section 3.1 to clarify that these figures are intended to illustrate the interaction between large-scale macroalgae cultivation and the background marine biogeochemistry.

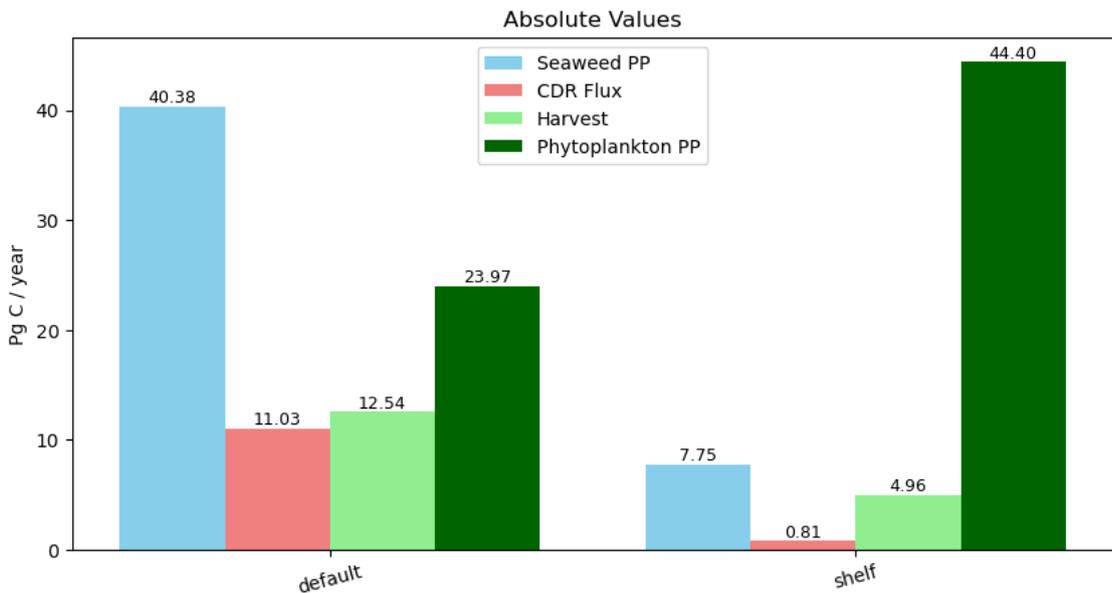
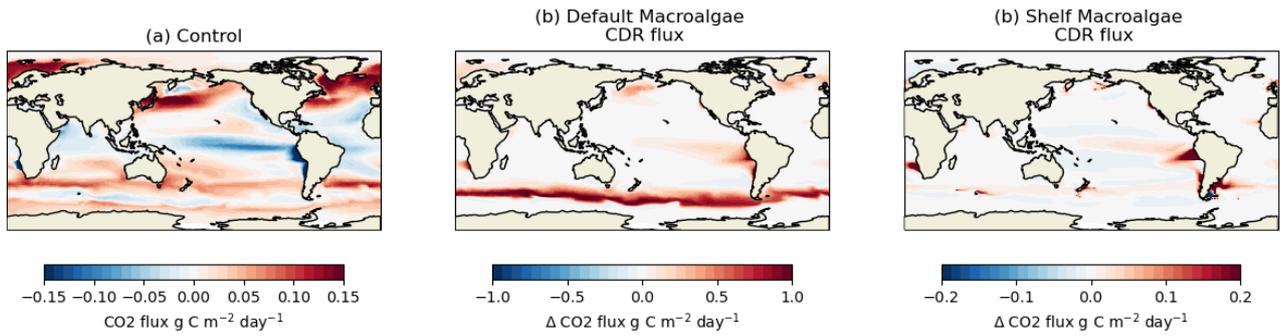
(line 269-272)

... Southern Ocean, and along the coast of Chile (Fig 2b, c, d, and 3). The spatial patterns of macroalgae, NPP, and nutrients shown here are emergent outcomes of open-ocean biogeochemical conditions within a coarse-resolution global model and should be interpreted as indicating potential cultivation areas and not as plausible regions for macroalgae farms. Many regions identified as productive for macroalgae would present extreme technological, logistical, and societal challenges.

307-315 Although these models are great at providing some thought into what may happen if we could potentially cultivate macroalgae at scales covering the entire ocean, I doubt that it is feasible and vastly overestimates the true potential of macroalgae aquaculture. If the model is conditioned on feasible cultivation areas, would the potential sequestration rate?

We agree with the reviewer that cultivation at global scale is not currently feasible and that such configurations should be interpreted as idealised “best case” scenarios. Our primary objective in this study is to explore the maximum CDR potential of macroalgae cultivation as well as the likely biogeochemical consequences at climate-relevant scales.

To directly address the reviewer’s question, we conducted an additional sensitivity experiment where we only allow macroalgae to grow in the shelf seas (anywhere where depth is < 200m). Under this constraint, simulated CO₂ flux increases by 0.81 Pg C / year, where the equatorial Pacific simulates the greatest flux (see Figures 2 and 3 below). It simulates a modest decrease in phytoplankton NPP by 4.34 Pg C/ year.



These results indicate that although the CO₂ flux is reduced, but the direction and nature of the biogeochemical response are preserved. We have included these findings in the Discussion to provide context on how limiting the cultivation at more practical area, such as the shelf seas, may scale the mCDR potential (lines 377-382 in the tracked change document):

... indicating that most fixed carbon is lost than durably stored. While our idealised experiments allow macroalgae cultivation over large oceanic areas, such configuration should be viewed as upper-bound scenarios. When cultivation is restricted to shelf-sea area (depth < 200m supplementary figures S8), simulated CO₂ uptake is reduced to 0.81 Pg C yr⁻¹ using default simulation condition, higher than that in previous EEZ study (0.21 Pg C yr⁻¹, Berger et al., 2023). This also suggests that constraining the spatial extent of cultivation affects the magnitude, rather than direction of biogeochemical response.

Reviewer #2 Evaluations:

Introduction Summary: The Additionality and Baseline Crisis

The manuscript employs the **NEMO-MEDUSA** global biogeochemical model to simulate the efficacy of macroalgae-based Marine Carbon Dioxide Removal (mCDR). The authors conclude that a global cultivation strategy could yield a 27% "net" sequestration efficacy. However, the fundamental scientific contribution of the paper is undermined by its treatment of the "Baseline."

A rigorous mCDR assessment must quantify **Additionality**: the carbon removed *above and beyond* what the natural ocean would have sequestered in the absence of intervention. In this study, the authors report a 27% efficacy while simultaneously observing a **50% suppression of natural phytoplankton communities**. This represents a massive "Ecological Opportunity Cost." If the seaweed merely replaces the sequestration function of a natural biological pump, the reported efficacy is a "Gross" figure that misleadingly suggests a climate benefit where there may be a net-zero or even negative carbon result.

We would like to thank the reviewer for going above and beyond in making sure that their points are clear with bullet point headings, **bold**, and *italicised* text.

We understand that our manuscript could be misinterpreted regarding the relative roles of macroalgae and the natural biological carbon pump. CDR efficiency from macroalgae NPP, (CDR_{effNPP} , equation 10), is a measure of additional air-sea CO₂ flux (relative to the control simulation) as a fraction of macroalgae NPP (based on Berger et al., 2023); meaning that the 27% figure already accounts for competition and displacement of the natural biological pump and hence inherently addresses the additionality issue raised.

As an aside, we assume that harvested biomass is actively processed for transportation to the seafloor so – unlike the natural biological carbon pump – experiences very little attenuation throughout the water column. As a result, for the same NPP in surface waters, our simulated macroalgae are more “efficient” than natural phytoplankton for carbon storage.

II. Detailed Technical Critique

1. The Thermodynamic Metric Error: NPP vs. NEP

A central technical deficiency throughout the manuscript is the conflation of **Net Primary Production (NPP)** with the drivers of air-sea CO₂ flux.

- **The Conceptual Flaw:** NPP represents the carbon fixed by the seaweed itself. However, the atmosphere is blind to NPP; it only "sees" the **Net Ecosystem Production (NEP)**, defined as $NEP = GPP - R_{community}$.
- **The Respiration Penalty:** Large-scale seaweed farms are not isolated carbon sinks; they are complex ecosystems that support high rates of community respiration, including organic matter exudation and microbial decomposition.
- **The Modeling Gap:** If the NEMO-MEDUSA implementation uses NPP-driven drawdown to calculate the pCO₂ gradient, it inherently ignores the carbon "leakage" back into the DIC pool from the farm's own respiratory community. The authors must explicitly state whether their flux calculations are driven by a true NEP deficit. Failure to account for the respiration of the farm's heterotrophic community results in a significant overestimation of the "hole" created in surface DIC.

The reviewer assumes that our air-sea CO₂ flux calculations are driven by NPP-based drawdown alone, ignoring plankton respiration and macroalgae loss. This is incorrect. Firstly, air-sea CO₂ flux is calculated independently of either the NPP or respiration / losses of phytoplankton and macroalgae. The air-sea flux only uses ambient temperature, salinity, DIC and alkalinity, together with the calculated gas transfer velocity. In a sense, the air-sea CO₂ flux in our model responds to the change in surface DIC after all production and consumption processes operate; not just NPP in isolation. The concern raised by the reviewer would be valid for observation-based calculations but it is not relevant for our modelling approach in this study.

Furthermore, our approach is consistent with the methodology of prior global macroalgae modelling studies in that has been published (Wu et al., 2023; Berger et al., 2023; Arzeno-Soltero et al., 2023), none of which employ an NEP attribution framework as a prerequisite.

Further evidence that our model captures net system carbon balance rather than gross NPP-driven drawdown is provided by the Fe limitation experiment. When there is no Fe supplementation, both macroalgae and phytoplankton NPP is reduced compared to the default simulation, and this results in ~0.2 Pg C yr⁻¹ increase in CO₂ flux relative to the control. This only occurs if the model is resolving the full system carbon balance including competitive and respiratory dynamics.

To make this more explicit, we have added the following clarifications in Method section 2.2 of the manuscript (lines 212-215):

Note that MEDUSA resolves biological respiration and remineralisation for both phytoplankton and macroalgae at every depth level and timestep. The air-sea flux of CO₂ is driven by the net change in surface DIC after all biological processes (i.e. production, community respiration, grazing, and remineralisation) have been considered, rather than by NPP alone. The net ecosystem production (NEP) signal is thus an emergent property of the model's coupled biological and chemical state.

2. Kinetic Decoupling: The "Slow Tap" vs. The "Leaky Bucket"

The authors attribute the 27% efficacy to physical transport—the "**Leaky Bucket**" model (consistent with Heane et al., 2023 and Ho et al.). This assumes that the carbon deficit sinks into the deep ocean before it can be "filled" by the atmosphere.

- **The "Slow Tap" Argument:** I contend that the primary rate-limiter is the **Kinetic Lag** of the gas transfer velocity (k). Chemical re-equilibration of the mixed layer with the atmosphere has a characteristic timescale (τ) of roughly **one year**.
- **Seasonal "Expiration":** Seaweed growth is a transient, seasonal event. As established in recent research regarding **non-equilibrium NEP deficits (e.g., Ito et al., 2025)**, the biological drawdown happens within a 3–4 month window.
- **The Physics of Failure:** By the time the atmosphere begins to respond to the seasonal pCO₂ drop, the bloom has ended, the mixed layer has deepened, or the "deficit" has physically reset. The 27% efficacy is not a result of "losing" carbon to the deep; it is a result of the atmosphere never having enough time to pay the "carbon debt" created by the seaweed. The authors must provide a sensitivity analysis of the **equilibration timescale versus the bloom duration** to justify their efficacy figures.

Unfortunately, despite thorough searching, we cannot find the Heane et al., 2023 reference the reviewer cited, and therefore cannot engage with it directly.

We apologise if the manuscript did not clearly explain this aspect of the model. The NEMO-

MEDUSA framework does not ignore the lags in air-sea CO₂ exchange. This is calculated prognostically at every timestep using MOCSY 2.0 carbonate chemistry routines (Orr & Epitalon, 2015 – stated briefly lines 100-101 in the original manuscript) and the gas transfer parameterisation of Wanninkhof (2014), meaning that the model explicitly calculates how quickly CO₂ can move between the ocean and atmosphere at each location and time, rather than assuming instant equilibration (see our response to Reviewer 1's comment on how air-sea CO₂ flux is calculated above). This is the normal convention for dynamic models of the type used here.

The reviewer's "seasonal expiration" argument applies to simplified box model studies, not to our continuous 20-year 3D coupled physics-biogeochemistry simulations. In NEMO-MEDUSA, any CO₂ deficit that is not equilibrated within the growing season does not disappear as suggested by the referee. Instead, it remains to draw CO₂ from the atmosphere when ocean circulation next brings that water back to the surface. The model therefore naturally captures these delays. We already acknowledge re-equilibration timescales as a relevant constraint in our introduction (lines 44-46), consistent with Bach et al. (2021).

However, we have elaborated further to remove any opportunity for misinterpretation and have added the following text to the discussion section 4.3 of the manuscript (line 461-466):

Furthermore, the rate of air-sea CO₂ gas transfer, parameterised following Wanninkhof (2014) as a function of local wind speed, introduces a natural lag between biological carbon drawdown and atmospheric CO₂ uptake. DIC deficits that persist beyond a single growing season continue to drive CO₂ uptake as surface waters are re-exposed to the atmosphere through seasonal mixed layer dynamics and circulation. This helps explain the regional variation in CDR efficiency seen in Figure 4c, whereby in the Equatorial Pacific, despite relatively high macroalgal NPP, shows lower CDR efficiency, while in the Southern Ocean with deeper mixed layer, keep low DIC in contact with the atmosphere for longer, which results in higher efficiency

3. Ecological Substitution: The Borum & Sand-Jensen Zero-Sum Constraint

The model treats macroalgae as an "additive" removal tool, which contradicts established ecological principles of competitive exclusion.

- **The Constant NPP Principle:** Following **Borum & Sand-Jensen (1996)**, total system NPP in marine environments is remarkably constant. When macroalgae are introduced, they shade and outcompete natural phytoplankton for light and nutrients.
- **The Iron Fertilization Fallacy:** The authors note a 74% growth reduction without iron supplementation. However, if iron is added, natural phytoplankton (which have higher surface-area-to-volume ratios) often respond faster, blooming and shading the seaweed.
- **The Substitution Penalty:** If the model replaces a natural phytoplankton community—which may have had its own sequestration efficacy—with a seaweed farm, the **Net mCDR** is only the *difference* between the two. The authors must present a "Net-Net" analysis: (SystemFluxSeaweed–SystemFluxBaseline). Reporting 27% efficacy while ignoring the 50% loss of natural workers is scientifically indefensible.

Our simulation shows that macroalgae can outcompete natural phytoplankton for light and nutrients, which is central to our study (see Results section 3.3 and Figures 3 and 6); the 50% decrease in phytoplankton NPP is not something we overlooked. This occurs as an interaction between the net growth rates of phytoplankton and macroalgae that are shaped by both growth and loss processes. In the case of macroalgae, it is assumed that they experience only a simple linear loss rate, while phytoplankton experience losses driven by interactive grazer populations.

Regarding the ‘iron fertilisation fallacy’; the reviewer suggests that adding iron would cause phytoplankton to bloom and shade the seaweed. Our results show the opposite dynamic: even with iron supplementation, phytoplankton NPP declines by ~50% because macroalgae consume the available dissolved inorganic nitrogen (DIN), leaving DIN the most limiting nutrient for macroalgae instead of Fe. The reason that macroalgae need this iron supplementation is because, all other things being equal, phytoplankton are more competitive at the generally lower iron concentrations that persist in the open ocean. By assuming that the iron requirement of our macroalgae is satisfied where they are grown, we alleviate this competition, allowing macroalgae to dominate in certain regions of the open ocean.

Our CDR efficiency metrics from the NPP equation (Equation 10) explicitly computes additional CO₂ flux relative to a control baseline that does not include macroalgae; meaning that the phytoplankton sequestration that would have occurred without intervention is already subtracted. This is exactly the “net-net” analysis that is mentioned in the reviewer’s comments. The 27% efficiency figure is therefore already accounts for phytoplankton NPP loss. Our approach follows the CDR efficiency method by Berger et al. (2023), who apply the same logic of computing CDR efficiency as the ratio of enhanced air-sea flux to macroalgal production while explicitly accounting for phytoplankton feedbacks. To avoid ambiguity, we have added the following clarification to the methods section (lines 251-252 in the tracked changed manuscript).

... DIC deficit within the grid cell has driven the CO₂ uptake. The calculation of CDR_{eff NPP} is therefore a net measure, incorporating macroalgal production, phytoplankton feedback, and air-sea carbon equilibration collectively (Berger et al., 2023).

As well as in the Discussion section 4 line 369-375 in the tracked changed manuscript:

... and is lower than a modelling cultivation study within EEZ (58%; Berger et al., 2023). It is important to note that the 27% CDR efficiency already accounts for the displacement of natural phytoplankton productivity. CDR_{eff NPP} measures the fraction of macroalgal NPP that results in additional CO₂ uptake by the ocean, relative to a control simulation without macroalgae (Equation 10, following Berger et al., 2023). The ~50% suppression of phytoplankton NPP reported in Section 3.3 is therefore not an additional loss to be subtracted from the 27% figure, it is already embedded within it. In other words, macroalgae cultivation under the default scenario replaces roughly half of the natural biological pump while delivering only 27% additional CDR, highlighting the modest net climate benefit relative to the scale of ecosystem disruption

4. The Carbonate Counter-Pump: The "Bach Critique"

The manuscript treats seaweed as a "soft-tissue-only" pump, ignoring the inorganic carbon cycle.

- **Epibiont Calcification:** Seaweed fronds are colonised by calcifying epibionts (bryozoans, tube worms). As highlighted by **Lennard Bach**, calcification releases CO₂ ($\text{Ca}^{2+} + 2\text{HCO}_3^- \rightarrow \text{CaCO}_3 + \text{CO}_2 + \text{H}_2\text{O}$).

The Ballast Crisis: Displacing calcifying phytoplankton (coccolithophores) removes the mineral ballast that allows organic carbon to sink rapidly. Without this "ballast," organic seaweed fragments remineralize in the upper ocean, returning CO₂ to the atmosphere much faster. The authors must incorporate an Alkalinity Budget to prove that the seaweed-dominated system actually lowers pCO₂ more than the coccolithophore-dominated baseline it replaces.

We have acknowledged in the discussion that carbonate chemistry penalty from epibiont calcification is not represented in the model (lines 394-396 in the original manuscript), and we agree that this process can offset macroalgae-driven DIC drawdown. Additionally, the PIC:POC ratio in Bach et al. (2021) may not be suitable for farmed macroalgae. Inclusion of this penalty would also reduce our already modest CDR efficiency estimates which would strengthen our main conclusion.

Regarding ballast crisis: MEDUSA does not explicitly resolve coccolithophores as a separate functional type, and the reviewer's concern about reduced ballasting efficiency under macroalgae-dominated condition is one of the sources of model uncertainty. However, the effect of reduction in ballasting efficiency would decrease CDR efficiency further and support our conclusion that large-scale macroalgal CDR has limited net climate benefit. We will provide more detail about this in the model limitation section in the discussion (line 480-487 in the revised manuscript):

Additionally, our macroalgae module lacks variable stoichiometry (Arzeno-Soltero et al., 2023), DOC release (Paine et al., 2021), and explicit macroalgal grazing or erosion (Wu et al., 2023, 2025). The module also does not represent calcifying epibionts that commonly colonise sargassum, and their calcification can offset CDR (Bach et al., 2021). Furthermore, MEDUSA does not resolve coccolithophores phytoplankton types, meaning that potential reduction in calcite ballasting due to the reduction in phytoplankton concentration, are not captured. These omissions would act to further reduce CDR efficiency. The absence of ...

(continued in line 500-502) Our results should be interpreted as a first order approximation of the biogeochemical consequences of large-scale macroalgae cultivation, and that representing these additional processes in future model developments will be important in estimating macroalgal CDR potential.

Summary verdict and actions required

Overall Verdict: This paper sits in a difficult middle ground. While it utilizes a sophisticated model (NEMO-MEDUSA) and expands the geographical scope of macroalgae mCDR beyond the typical EEZ boundaries, it does not offer a significant leap in mechanistic understanding, whilst inadvertently supporting current misconceptions on the role of the air sea flux and ignoring the impact of biological calcareous production.

We would like to politely disagree with the reviewer's verdict here. We believe some of the concerns raised stem from a lack of clarity in how the modelling framework and carbon accounting were described in the original manuscript, and we have now expanded the text to better explain these aspects. The biogeochemical processes underlying these calculations follow well-established approaches used in 3-D ocean biogeochemical models (as clarified above) and we already explicitly acknowledged the processes that were not explicitly represented, whilst acknowledging that if they were, they would reduce CDR efficiency even further, and in turn would strengthen our conclusions. Furthermore, the paper does not aim to advance 'mechanistic understanding' but rather assess the potential climate benefits and biogeochemical impacts of large-scale macroalgae production.

(Note our comments about the air-sea flux and CaCO₃ production above.)

1. Lack of Novelty:

The authors essentially "re-discover" the limitations already voiced by Prof. David Ho and Philip Boyd regarding iron limitation (74% drop) and low air-sea efficiency (27%). By modeling "global" seaweed farming, they are merely showing that the open ocean is an even less efficient place for mCDR than the coastal zones, which is an expected result rather than a novel insight.

We respectfully disagree that our findings are merely a reconfirmation of existing results. While iron limitation and low CDR efficiency have been noted in previous studies (e.g. Berger et al., 2025, Paine et al., 2023), the finding that Fe limitation causes net outgassing of CO₂ relative to the control simulation (due to macroalgae-driven Fe depletion that suppress both phytoplankton and macroalgae) is novel. Our results emphasise that without the Fe supplementation, large-scale macroalgae farming is likely futile for carbon sequestration.

Furthermore, our exploration of different harvesting thresholds demonstrated that the harvest threshold substantially modifies both CDR efficiency and deep-sea oxygen depletion, are not results that has been reported from prior literature. Our work is also the first to systematically compare multiple harvest protocols, biomass extraction strategies, and Fe limitation within a single modelling framework, and to quantify the consequences for seafloor deoxygenation, nutrient redistribution, and lower trophic level. We are confident that these contributions represent a meaningful advance beyond existing studies.

These points are addressed in detail in our responses above and in the revised manuscript text.

2. Physical and Chemical Omissions:

The manuscript ignores two major developments in recent literature and a category error:

- The Carbonate Counter-Pump within oceanic seaweed ecosystems: As established by Lennard Bach, you cannot model macroalgae sequestration without an alkalinity budget from calcifying epibionts. Furthermore this is compounded in regards to C mitigation relative to baseline in the replacement (partial to total) of areas with coccolithophore production that likely inflates the reported C mitigation efficacy.
- Non-Equilibrium Dynamics: The paper relies on the "standard model" of down welling as the cause of low efficiency. However, the true bottleneck, is the permanent kinetic lag of CO₂ invasion as supported by my own work on seaweed and blue carbon systems and citation therein (Nishihara et al. 2025), the driver of this through seasonal surface CO₂ deficit variation that requires a input resolution of less than 1 the month, not used in their application of the NEMO-MEDUSA model. All this leading to a misunderstanding that down welling is the primary driver of sequestration inefficiency is primarily down welling. Thus leading to wrong conclusions on where of seaweed C sequestration efficiency would be the worst or best.
- The use of NPP as the biological that ignore community respiration outside algal metabolism, when it needs to be NEP (Gallagher et al. 2022).

We thank the reviewer for their summary assessment. Reviewer's concern on NEP vs NPP, carbonate chemistry and epibionts, and kinetic re-equilibration have been addressed in points 1, 2, and 4 above, and we refer the reviewer and editor to those responses above. We have also responded to reviewer's recommendation below:

As addressed above, the reviewers' concerns outlined above are due to a misunderstanding by the reviewer of how 3D biogeochemical models, and the subsequent calculations in this study (and other mCDR modelling studies), already address these issues as described in points 1 and 2 above. Furthermore, as addressed in point 4, we have acknowledged that calcifying epibionts are not

represented in the model, consistent with prior studies (e.g. Berger et al. 2023, Wu et al., 2023; 2025, Arzeno-Soltero et al., 2023). We have already advanced several aspects of macroalgae modelling in this study (Fe limitation/supplementation, harvesting thresholds and biomass extraction strategies) and suggest exploring the impact representing the calcifying epibionts is an area for future studies to address.

Recommendation:

In its current state, the paper risks being a "replication study" that repeats the structural errors of previous models (treating the ocean as a leaky bucket rather than a kinetically limited system). I have recommended a Major Revision.

We thank the reviewer for the detailed comments, as we have explained in the summary verdict, we respectfully reject this framing that our study is only a replication of prior findings. Our study extends prior large-scale macroalgae modelling by incorporating multiple harvesting threshold, Fe limitation, biomass extraction, and increasing higher non-harvest loss scenarios.

To merit publication, the authors must move beyond "gross" sequestration figures and provide a Net System Analysis that accounts for:

- Surface water community respiration for NEP as the biologically driven CO₂ deficit ((Ito & Reinhard 2025)

NEMO-MEDUSA explicitly resolves the full biological carbon cycle, including phytoplankton production, plankton respiration, and other biogeochemical processes at every depth level and time step. The air-sea CO₂ flux is computed using MOCSY 2.0 carbonate chemistry routines (see our response to Reviewer #1 on details on how air-sea CO₂ flux is estimated, and our response to point 2) which responds to changes in surface DIC driven by plankton, macroalgae, and other biogeochemical processes as well as a general increase in DIC driven by invasion of the ocean by anthropogenic CO₂ from the atmosphere.

NEP comes from the model's coupled biological and chemical state rather than being prescribed or ignored. We have made this clearer in the revised manuscript (cf. our response to point 1).

- The displacement of natural phytoplankton (Borum & Sand-Jensen 1996) "zero-sum" NPP.

The displacement of natural plankton is not ignored; it is dynamically simulated through MEDUSA. Our model explicitly resolves nutrient competition between macroalgae and phytoplankton at every grid cell and timestep, producing the ~50% phytoplankton NPP suppression we report (see abstract and results section 3.3). We have, however, added explicit text clarifying that our CDR_{effNPP} metric already reflects net efficiency accounting for this displacement, to avoid any ambiguity. Please see our response in point 3.

- The carbonate chemistry penalty (Bach et al. 2021).

Again, the carbonate chemistry penalty arising from calcifying epibionts is acknowledged explicitly in our model limitations (lines 394-396 in the original manuscript) and the PIC:POC ratio in Bach et al. (2021) may not be suitable for farmed macroalgae. We agree this process could partially offset macroalgae-driven DIC drawdown at the farm scale, and we will add this into the discussion and clarification that our model is just a first order approximation. We have addressed this concern in point 4 above.

The kinetic re-equilibration lag on seasonal scales (Ito & Reinhard 2025; Jiang et al. 2019) for which I add my own daily simulation in a supplementary document to clearly illustrate surface water dynamics. This is a figure from our unpublished article currently in submission, using a similar but higher resolution and likely NEP for seaweed variation.

While we appreciate the intent to illustrate a point, we would respectfully flag to the editor that we consider it unfair to be asked to benchmark our work against, or respond to, results that have not yet undergone independent peer review and are provided without context of the model used and assumptions included. We defer to the editor's judgment on this matter.

If the authors cannot integrate these non-equilibrium and competitive dynamics, the paper's "global potential" maps are more misleading than helpful for the mCDR.

We are committed to strengthening the discussion of kinetic and carbonate chemistry constraints, as these are legitimate areas for improvement. However, we maintain that the core methodology is sound and that competitive phytoplankton displacement is already dynamically represented.