

Comments on GMD-2024-94: *Sunburned plankton: Ultraviolet radiation inhibition of phytoplankton photosynthesis in the Community Earth System Model version 2*
2 Authors: Coupe et al.

General Comments – The authors have implemented for the first time an earth system model that includes the effects of solar UV irradiance on the photosynthesis of marine phytoplankton. Although there have been several modeling exercises that address the effect of UV inhibition of photosynthesis on, e.g., daily areal productivity for global or regional (e.g. Southern Ocean) basis, this is the first time those responses have been integrated into a full ecosystem model with the provision of feedback effects and shifts in taxonomic composition. This new model is potentially useful in inferring what effects UV currently has on the marine pelagic ecosystem as well as how these effects may change in response to various extreme events or climate manipulations. An additional use case would be to compare the model output for scenarios with and without the controls on ozone depleting substances imposed by the Montreal Protocol. Such global assessments of the “world avoided” have thus far only been conducted for carbon cycling in terrestrial ecosystems (Young et al. 2021).

While I applaud the work of the authors in structuring the model, the implementation of the biological weighting functions and penetration of weighted UV radiation has several deficiencies. I expect that the model can be corrected to address these problems (detail provided below), so that the modeling and assessment community can have a CESM2-UVphyto that is consistent with our current understanding of UV effects on phytoplankton.

Thank you for your detailed and careful review of our manuscript! In the revised manuscript, we have corrected the model to address the previous deficiencies in the biological weighting functions and the penetration of UV radiation. We include a detailed response to your comments below. The full revised manuscript will be made available following the end of the discussion period.

Specific Comments

- 1) A general point that should be made clear to any user of the model is that sensitivity to inhibition by UV irradiance is a physiological characteristic that is as variable as any other parameter of phytoplankton photosynthesis. Sensitivity is variable mainly because net inhibition reflects that balance between damage and repair processes (e.g. Neale and Kieber 2000). Variability on the damage side primarily derives from physical characteristics – e.g. the optical characteristics and cell dimension – these most often vary in a narrow range for any one taxa. However, repair processes can vary considerable depending on growth conditions. In this version of CESM2-UVphyto, Biological Weighting Functions (BWFs) are fixed irrespective of growth conditions

(except for CO₂ – see below). This is an inconsistency in the code since the MARBL model does incorporate photoadaptation of photosynthesis in general through the C:Chl ratio, responding to growth irradiance, temperature and nutrients. It shouldn't be surprising that sensitivity to UV inhibition is also affected by these factors and there are many studies that confirm this beyond the studies cited for the model (see bibliography below). Where variation is known, e.g. for temperature and growth irradiance (cf. Neale and Thomas 2016), the code should account for it. If UV inhibition response is known only for one growth condition, the model should warn of increased uncertainty for predictions beyond the experimental conditions used for determination.

The biological weighting functions selected for UV inhibition in the model do not vary depending on temperature or PAR. Such complexity is not possible for all BWFs, as BWFs are often available at only one or two temperatures. In response to this comment, we have added text to the Discussion section of the manuscript explaining the limitations of the current version of the model and possible next steps to add more complexity.

“We caution that the model is somewhat sensitive to the exact BWF employed and because the PFTs in MARBL represent many different types of phytoplankton while the BWFs are based on single species, there is no "correct" BWF. Furthermore, there is a limited temperature range at which BWFs are reported, typically between 20C and 26C, affecting model performance at very cold temperatures.”

- 2) The one condition for which the model varies sensitivity to UV is in relation to atmospheric CO₂, which changes the pCO₂ and pH of ocean water. Ironically, the BWFs for the microalga chosen to simulate the effect of changing CO₂ show no evidence that they are affected by elevated CO₂. Lorenzo et al. (2019) compared the BWFs of *E. huxleyi* grown at equilibrium with atmospheric CO₂ of 400 and 800 ppm and found no difference even though there were changes in the coccoliths. Xu et al (2016) observed somewhat contrasting results in that a calcified strain was more resistant to UV than a naked strain. They concluded that coccoliths have an effect protecting against UV, however the experiment was not controlled in the sense that there were several differences between the + and – UV treatments, besides UV (including strain, PAR level, variability of exposure). These differences don't exclude that coccoliths perform a screening function, however the study of Lorenzo et al was performed under controlled conditions so that CO₂ was the only factor that varied. In this case, the changes in coccoliths were insufficient to affect sensitivity to UV or if the change in coccoliths did allow more damaging UV to reach the cell, the effects were compensated by enhanced repair capabilities (this is discussed by Lorenzo et al). In summary, it would be inappropriate to vary the E_{inh} (* omitted for convenience) computed from the Lorenzo et al BWF according to the PIC/POC ratio when Lorenzo et al did not observe an effect. As an aside, other taxa do show increased sensitivity to UV under CO₂ enhancement and it would be interesting to evaluate their responses in the context of the model (see Sobrino et al 2008).

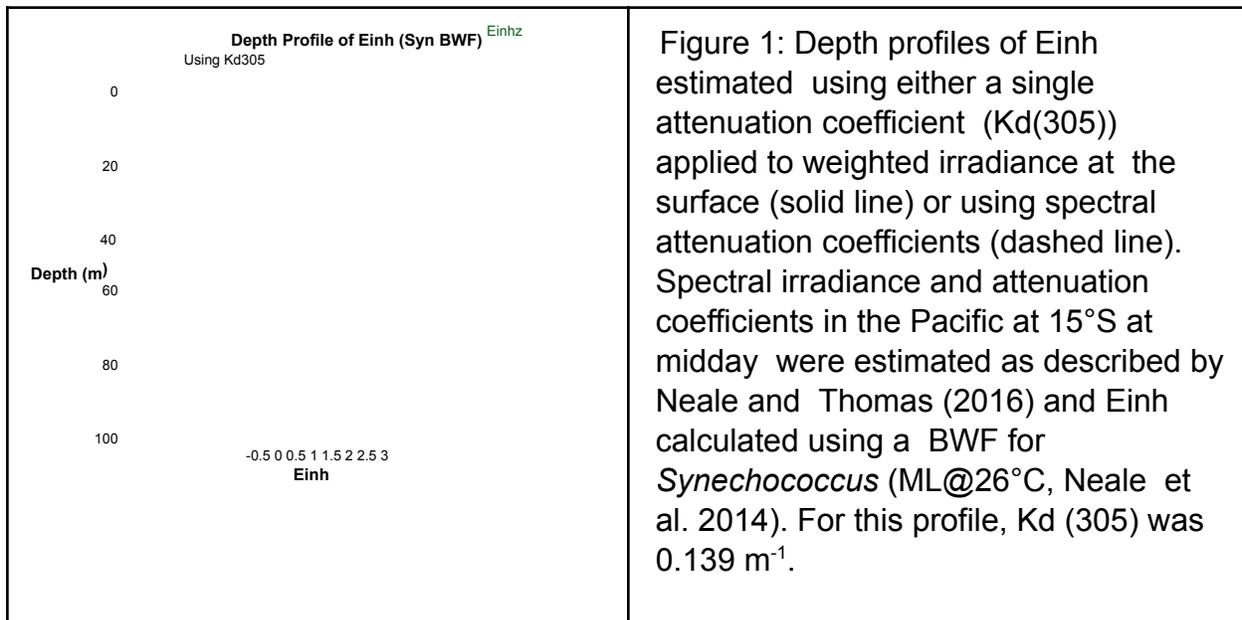
In principle, I expect that the model code can be changed to accommodate this variability, which I encourage the authors to do. But I also recognize that the BWFs used in the case studies shown could be regarded as a “proof of concept” choices. This is defensible as long as it is made clear that results could be quite different for other choices, even for taxa within the same PFT group. However, independent of the choice of BWF, there are several steps described in the calculation of inhibition of photosynthesis section that are incorrect and lead to results that are inconsistent with current understanding of UV effects.

The species used to construct the coccolithophore PFT in MARBL is much more lightly calcified than that used by Lorenzo et al. in their 2019 study. While Lorenzo et al. (2019) did not observe a decrease in PIC/POC in response to increasing CO₂ in their heavily calcified strain, experiments conducted with other species indicate a decline in PIC/POC with increasing CO₂ which has consequences for UV sensitivity of coccolithophores (Xu et al, 2011; Guan et al., 2010). Thus, in the version of CESM2-UVphyto that we use for our simulations, we maintain the PIC/POC scaling for UV sensitivity. We note that this feature can be toggled on or off in the model for other users.

In response to this comment, we have revised the text to read:

“the species used by Lorenzo et al. (2019) is heavily calcified, unlike the species used to construct the coccolithophore PFT in MARBL. We include a scaling enhancement of UV inhibition as a function of coccolithophore shell thickness to the model which can be toggled on by the model user.”

3) The propagation of E_{inh} through the water column cannot be approximated with the attenuation of a single wavelength (Eqs 2 and 3). Although it is often used as a proxy for the attenuation of DNA damaging UV-B, the attenuation coefficient at 305 nm is inappropriate for propagating $E_{inh}(z)$ because most of the weight derives from UV-A. As a result, E_{inh} propagated with $K_d(305)$, declines with depth much faster than that calculated with a fully spectral resolved $K_d(\lambda)$, as shown in this example for clear oceanic water :



The depth to which UV inhibition affects photosynthesis in clear ocean waters is much deeper than 16 m (see also Fig. 2 in Neale and Thomas 2016). The effective $K_d(z)$ ($= -\ln(\text{Einh}(z+1)/\text{Einh}(z))$) in this example is similar to that of $K_d(\lambda=327\text{nm})$ at the top of profile but changes (decreases) progressively to be similar to $K_d(\lambda=388 \text{ nm})$ at 100 m, with about 2.4x change in apparent K_d over the profile.

We thank the reviewer for this detailed analysis of the shortcomings of our current attenuation scheme. Ideally, we would have high spectral resolution of E^*_{inh} for use in the oceans. However, because of computational resources there are limitations regarding the number of fields that can be passed from the atmosphere to the coupler and to the ocean at each timestep. It was this constraint that informed the initial design.

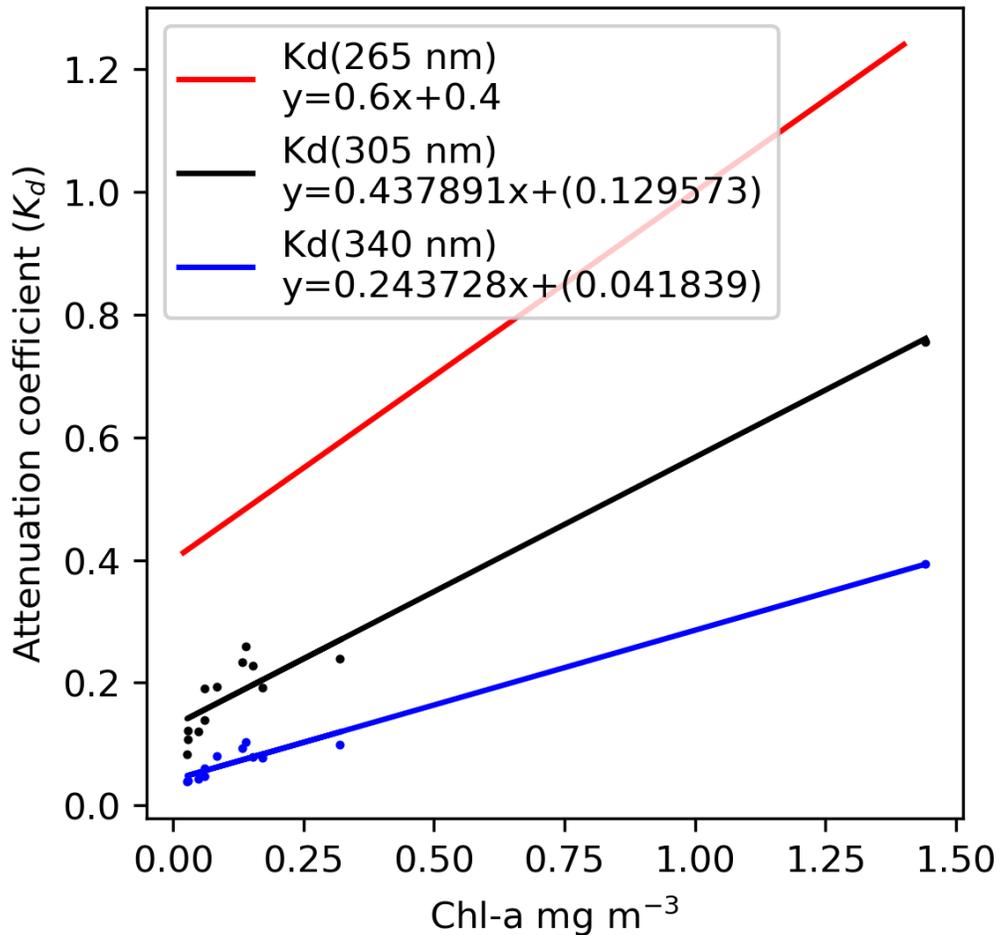
We have refined the spectral resolution of E^*_{inh} by separating E^*_{inh} into UV-A, UV-B and UV-C components. New attenuation coefficients for the different components of E^*_{inh} are detailed in the response to Specific Comment #4.

- 4) Therefore, a more wavelength resolved approach is needed to propagate Einh. The values of Overmans and Agusti (2020) for coral reef areas in the Red Sea are inappropriate to apply over the whole ocean (Eq 2). Many areas of the ocean have more UV transparency than the Red Sea. Tedetti and Sempéré (2007, Table 2) reviewed global measurements of UV penetration and report that most open ocean waters have, e.g., 10%UV-B depths > 8 m. The maximum 10%UV-B depth possible from the Overmans and Agusti equation is $2.3/.29 = 7.9 \text{ m}$. UV penetration is higher in the open ocean because it is further from land and has lower concentrations of colored

dissolved organic matter (CDOM) than the Red Sea. CDOM is more important in determining UV transparency than Chl. One possible approach to a more representative spectral K_d is to use the equation of Lee et al (2013) (see their Eq. 5), estimating the IOPs of absorption and backscattering based on MARBL parameters – mainly Chl, POC and DOC.

The chlorophyll approach was chosen because the existing formulation for visible light propagation in the model uses chlorophyll information. Because of the high correlation between dissolved organic matter and chlorophyll in the open oceans in our model, we maintain the use of chlorophyll but have abandoned the Overmans and Agusti (2020) approach. To better represent open ocean conditions, which comprises the majority of grid cells in our model, we constructed new attenuation coefficients based on the chlorophyll and K_d data in Tedetti et al. (2007) for UV-A and UV-B radiation. Because there is very little work studying UV-C radiation attenuation, Smith and Baker (1981) attenuation coefficients for clear seawater were used to construct the UV-C attenuation coefficients. A figure showing the Tedetti et al. (2007) data and regression lines is shown below.

Regression of CHL onto Kd based on Tedetti et al. (2007)



Attenuation coefficients (K_d) have now been changed to the following, where x is chlorophyll and K_d is the attenuation coefficient:

UV-A radiation, K_d(λ~340 nm): $K_d = 0.243728x + 0.041839$

UV-B radiation, K_d(λ~305 nm): $K_d = 0.437891x + 0.129573$

UV-C radiation, K_d(λ~265 nm): $K_d = 0.6x + 0.4$

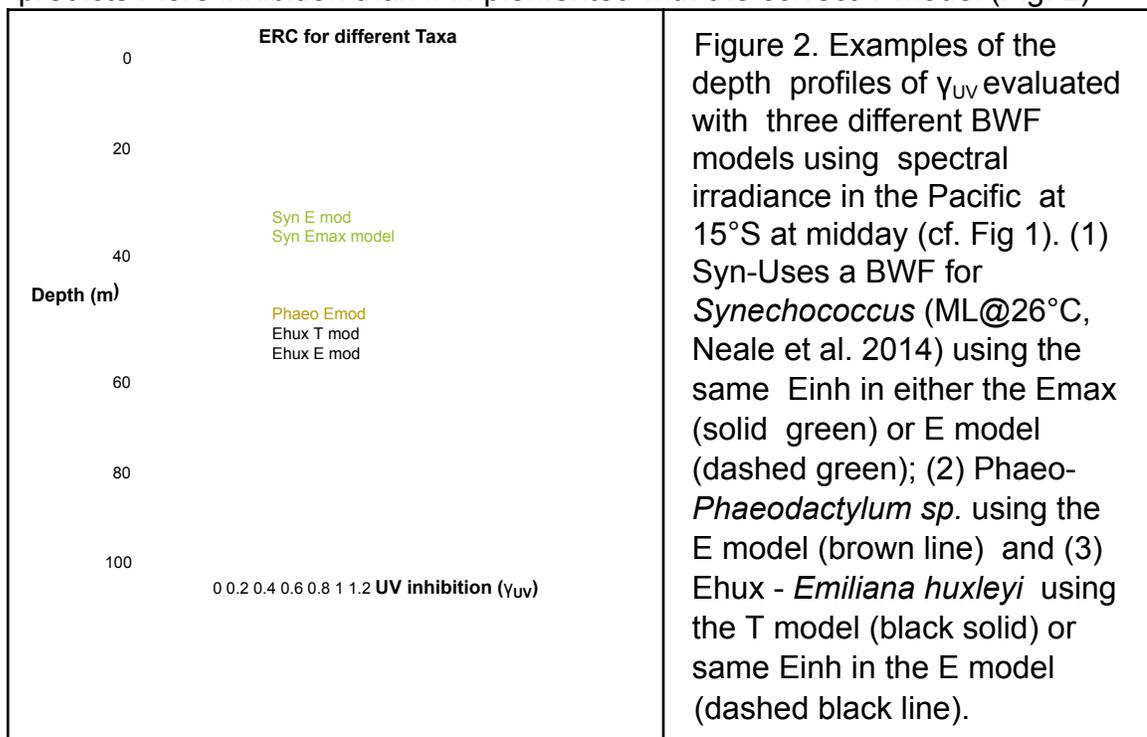
Using Smith and Baker (1981) values for pure seawater as a reference, the attenuation coefficient at the selected wavelengths are now similar for the minimum chlorophyll value in MARBL (0.02 mg m⁻³). Only K_d(340 nm) has slightly lower attenuation than the values determined in Smith and Baker (1981). However, because of the large weight of wavelengths above 340 nm, K_d(340) is likely closer to K_d(340 to 360 nm). Below are the Smith and Baker (1981) values, as a comparison:

K_d(340 nm)=0.0637

K_d(305 nm)=0.12

K_d(265 nm)=0.4

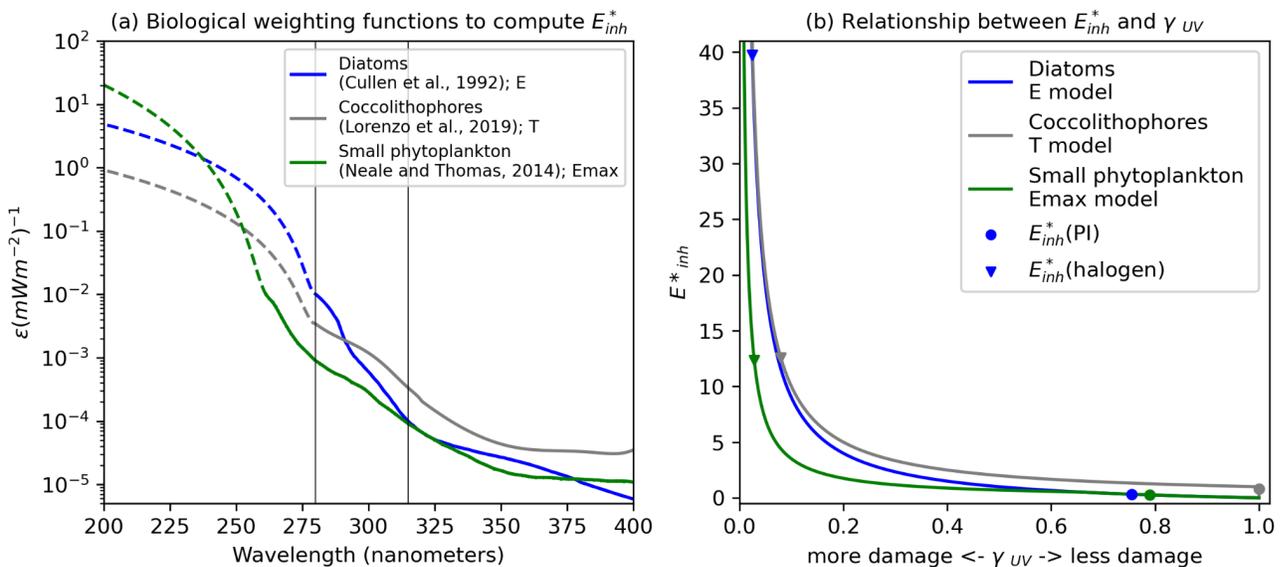
5) BWFs in the literature are part of specific integrated photosynthesis-irradiance relationships (BWF/P-I models), and only correctly estimate UV inhibition if implemented using the relationship for which they were defined. There are three BWF/P-I models : E, T and Emax (see comparative discussion in Lorenzo et al. (2019), and each BWF used in the CESM2-UVphyto case studies uses a different linked model. Particularly important is the difference between the E model used for the Diatom (*Phaeodactylum*) BWF ($1/[1+Einh]$ dependence) and the T model used for the Coccolithophore (*E. huxleyi*) BWF ($1/Einh$ dependence). Evaluating UV inhibition by substituting the *E. huxleyi* Einh into the E model predicts more inhibition than if implemented with the correct T model (Fig. 2)



For the T model prediction of *E. huxleyi* inhibition (Fig. 2), there is a sharp decline in inhibition with depth as this model was optimized to best predict responses at high exposure. The same Einh evaluated with the E model has lower γ_{UV} (more inhibition) and penetrates deeper. Lorenzo et al acknowledged that there probably is some inhibition at lower exposures (and deeper in the water column), but this could not be

resolved given the variability of the laboratory measurements, so below a certain depth (23 m in the above) there is no effect. In the example, the overall inhibition of midday productivity over the upper 100 m, given the P-I parameters in Lorenzo et al, is only 11% with the T model, but increases to 30% if the T model E_{inh} is used to predict γ_{UV} using Equation 4 (E model). This directly impacts conclusions drawn from the reported case studies that coccolithophores are the most sensitive to inhibition by UVR. Higher E_{inh} , per se, doesn't mean more inhibition if the models are different.

We thank the reviewer for pointing out this crucial mistake in the model. We now have updated the model using E, T, or E_{max} when appropriate. This, in conjunction with altering the attenuation coefficients, has slightly modified the results. A new figure has been added that relates E^*_{inh} and γ_{UV} for all of the different models employed, as a subpanel in Figure 1.



New version of Figure 1.

6) On the other hand, for the small prokaryotes, *Prochlorococcus* and *Synechococcus*, response at low exposure (which varies as $1/[1+E_{inh}]$) could be resolved and distinguished from that at high exposure ($1/E_{inh}$ dependence), the two responses are combined in the E_{max} model (Neale et al 2014). The BWF/PI for both Pro and Syn use the E_{max} model, which in this case leads to more inhibition for the $E_{inh}(PI)$ case compared to using the $1/[1+E_{inh}]$ form over the whole water column (Fig. 2). Use of the correct model combined with more accurate E_{inh} propagation should result in much higher relative effect of UV on ocean productivity for $E_{inh}(PI)$ than the $\sim 1\%$ effect in the reported case studies. The cited range of 7-28% inhibition reported by Neale and Thomas 2016 is the inhibition of integrated

midday production by UV (vs only PAR) in their simulations of the Pacific for current conditions, not what was observed in the laboratory. Similarly, estimates of around 7% inhibition of daily integrated production by UVR have been obtained by other approaches, e.g. Cullen et al. (2012) and Moreau et al. (2015).

We employed the updated BWF models with attenuation at a higher spectral resolution, as suggested, and found an increase from the 1% reported effects, especially in the surface oceans. The manuscript has been updated to reflect the new results.

7) The BWF function chosen for small phytoplankton is for *Prochlorococcus*, which is much more sensitive to inhibition by UV radiation than other picophytoplankton (Neale and Thomas 2016). It is better consider Pro a separate case. The BWFs for *Synechococcus* is probably more representative of picophytoplankton overall as well as diazotrophs.

We thank the reviewer for this suggestion. We have adopted the new *Synechococcus* BWF using the Emax model from Neale and Thomas (2014) in the new version of the model. This can be seen in the new Figure 1.

8) Equation 1 should include a term for inhibition by PAR ($\epsilon_{\text{PAR}} * E_{\text{PAR}}$ cf. Eq. 3 in Neale and Thomas 2016). PAR inhibition is significant for the cases of *E. huxleyi*, *Prochlorococcus* and *Synechococcus*, and other published BWFs. No PAR inhibition was defined for *Phaeodactylum*, that is partly related to the lower E_{PAR} exposures used in this first experimental determination of the BWF.

We thank the reviewer for bringing the importance of PAR inhibition to our attention. We examined the PAR fields in our simulations and do not find sufficient conditions for significant PAR inhibition. The existing MARBL photosynthesis calculation is already intended to capture phytoplankton behavior at higher PAR levels. We have added a sentence that makes mention of PAR inhibition, but we clarify that it will not be a significant factor in the pre-industrial simulations presented in this manuscript nor future asteroid impact simulations, which exhibit a strong decline in PAR.

“ E_{inh} can include a PAR inhibition term in its calculation, which is included in some laboratory studies (Neale et al., 2017); this term is ignored due to the lack of spatial or temporal frequency of very high PAR in these simulations or in anticipated future asteroid impact simulations. “

9) Elevated UV radiation. Because most inhibition is caused by UV-A radiation, E_{inh} at the surface for known BWFs will never be increased by a factor of 20 vs $E_{inh}(PI)$, even if 95% of stratospheric ozone is destroyed (total ozone column would be reduced by a lower fraction as the increased penetration of UV-C will form ozone at lower altitudes). Thomas et al (2015) treated the case of a gamma-ray burst resulting, briefly (months), in a strong depletion of column ozone by 70% in the region of the strike. At most, this increased the $E_{inh}(0)$ by a factor of 2.63, based on the Phaeo BWF which has probably the largest ratio of sensitivity to UV-B vs UV-A. The multiplier will be less for almost all other phytoplankton especially when PAR inhibition is included. The effect of a gamma-ray burst on Integrated production at midday was also evaluated for *Synechococcus* and *Prochlorococcus* (Neale and Thomas 2016b) and ozone depletion of 70% resulted in at most 3% additional inhibition (vs normal ozone) to the 1% depth of PAR and 7% additional inhibition of productivity integrated over the mixed layer.

We agree that the $E_{inh}(20x PI)$ values are overly simplified and may produce unrealistic E_{inh} values. Instead of this simplified approach employed in the previous version of the manuscript, we re-ran the model with a fully coupled high-top atmospheric model with full stratospheric chemistry. The new simulation included halogen amounts comparable to the Chicxulub asteroid impact, 117,000 Tg, as estimated by Toon et al. (2016). We now include this simulation in Materials and Methods with a forcing that is defined as $E_{inh}(\text{halogen})$ for the ocean-only simulations. However, we find that the E_{inh} values for these simulations are even greater than 20x $E_{inh}(PI)$ for small phytoplankton and diatoms, but not coccolithophores. Increased UV-B radiation, especially in the wavelength range where the BWF curves increase exponentially as a function of decreasing wavelength, is responsible for this. In this case, total column ozone is depleted by more than 95%. This is an extreme upper bound test case, where even UV-C radiation reaches the surface. We intend to use this model to test UV radiation after the K-Pg boundary in future work. In response to this comment the manuscript now reads:

“We conduct 5 year simulations to explore the modeled biogeochemical and ecological response to extremely high levels of surface UV radiation. Halogens equivalent in quantity to the Chicxulub asteroid impact at the K-Pg boundary (Toon et al., 2016) are injected into the stratosphere. The halogen injection includes hydrogen chloride and hydrogen bromide and is intended to mimic an upper bound of a possible surface UV radiation perturbation. At the same time, the halogens are unlikely to block visible or ultraviolet radiation from reaching the surface and will minimize changes to other aspects of the climate, circulation feedbacks in response to depleted ozone notwithstanding. This case is referred to as $E_{inh}(\text{halogen})$. A fully coupled simulation is run for two years and coupler forcing is used to generate a five-year offline simulation; for simplicity, years 3-5 of the offline simulation are repeated versions of

year 2 forcing.”

- 10) Yet another approach is needed for polar phytoplankton, for which low light and temperature can result in very low repair rates such that in some cases (mainly deeply mixed zones), inhibition is time dependent (see Neale et al 1998, Smyth et al 2012). Probably polar oceans, especially S. Ocean inside ice-limit, should be treated as a special case.

We agree that treating polar phytoplankton separately would be the most accurate way to simulate their response to changes in both PAR and UV radiation. MARBL, in its current configuration, is not suited to treat polar phytoplankton separately or to include a time dependent inhibition. This would likely require adding a fifth phytoplankton functional type. Text has been added to the revised manuscript that addresses the simplified nature of our model:

“Because of the diversity of the phytoplankton contained within the small phytoplankton functional group, phytoplankton in high latitude regions that are often highly temperature and light limited may not be as well represented in this model. “

- 11) Finally, the CESM2-UVphyto model assumes that the only effect of UV on phytoplankton is through inhibition of photosynthesis. However, UV (more specifically UV-B) also directly damages DNA, inhibiting growth. Too little is known to quantify the importance of this mode of UV effect on a global basis, still it should be recognized that it could be important (see Andreasson and Wangberg 2007).

We have made sure to include in the text that UV can directly damage DNA and cause long-term effects that are not represented. This can be found in “Discussion”:

“BWFs are typically determined from shorter term growth inhibition, which may not reflect effects of direct damage to DNA over longer timescales.”

Summary – The model needs extensive revision after which the case studies can be re-run. At that point the results and conclusions can be re-examined and re-written as needed. Detailed reviews of those sections will be provided then.

Minor and Technical Comments

Line 95 Although stratification has intensified, surface mixed layer depths are not increasing, contrary to the expectations of Gao et al. (2019). See discussion in Neale et al. (2023)

We have modified this discussion on global warming, stratification, and UV exposure to include nuance about present and future trends in mixed layer depths.

“Finally, marine phytoplankton exposure to UV radiation **may increase** in some regions as anthropogenic climate change warms the Earth's surface, representing a compounding threat. The warming of the Earth's surface in regions where wind speeds do not increase may increase the density gradient in the upper ocean.”

Figure 1 The text in several places states limits to UV-B as 280-315 nm, but this plot has the division between the bands at 320 nm

Figure 1 has been modified so that the bands are instead at 315 nm.

Line 230 Supplemental Table 1 only lists weights up to 327 nm

Supplemental Table 1 has been extended to the full wavelengths.

Line 230 Relative to the originally published BWFs, weights have been both interpolated and extrapolated.

BWFs need to be interpolated to the atmosphere model grid to use the weights. This has been clarified in the text. Extrapolation to UV-C wavelengths was necessary because they were not reported in all of the published BWFs, yet based on preliminary simulations of the K-Pg impact, UV-C radiation may be important for UV damage. We used information from the literature about the one BWF that did report UV-C damage information to extrapolate. This information has been added to the methods.

“A look-up table is provided in Supplemental Table 1. Wavelengths are interpolated to the bounds provided in this table to calculate spectral integrals”

“Not all of the employed BWFs extend into wavelengths below 280 nm (UV-C radiation). While UV-C radiation is a non-factor in recent history, it may become relevant after a cataclysmic asteroid impact. To account for UV-C radiation damage, BWFs are extrapolated to 200 nm, as indicated by dashed lines in Figure 1a.”

Line 265 As mentioned above, Lorenzo et al. 2019 did not find an effect of PIC/POC ratio on the BWF. In any case, the treatment effect found by Xu et al (which could be

UV as well as other factors) is more accurately defined as $3.5/2=1.75$, since the calcified strain grew twice as fast as the naked strain under PAR-only incubator conditions.

We have modified the text to clarify this as an optional feature which can be turned on and off. In the text, we elaborate on the effects of having this PIC/POC scaling feature.

As suggested, we modified the PIC/POC scaling factor from 3.5 to 1.75 to isolate UV effects only (and not PAR effects). As a result of this modification, coccolithophore decline in response to UV radiation has been moderated.

Line 520 Arrigo 1994 – journal name missing

The journal name has been updated.

Line 620 Neale and Thomas GCB, publication year is 2016

The year has been updated to 2016.

Respectfully submitted,

Patrick Neale
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