

Sunburned plankton: Ultraviolet radiation inhibition of phytoplankton photosynthesis in the Community Earth System Model version 2

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Abstract. Ultraviolet (UV) radiation can damage DNA and kill cells. We use laboratory and observational studies of the harmful effect of UV radiation on marine photosynthesizers to inform the implementation of a UV radiation damage function for phytoplankton photosynthesis in a modified version of the Community Earth System Model version 2 (CESM2-UVphyto). CESM2-UVphyto is capable of simulating UV inhibition of photosynthesis among modelled phytoplankton and ocean column penetration of UV-A~~and~~, UV-B, and UV-C radiation. We conduct a series of simulations with CESM2-UVphyto using the Marine Biogeochemistry Library (MARBL) ecosystem model to ~~calibrate estimates of~~ understand the sensitivity of phytoplankton productivity to UV radiation. Results from the simulations indicate that increased UV radiation shifts the vertical distribution of phytoplankton biomass and productivity deeper into the column, causes a moderate decline in total global productivity, and changes phytoplankton community structure ~~to favor diatoms~~. Our new CESM2-UVphyto model configuration can be used to quantify the potential ocean biogeochemical and ecosystem impacts resulting from events that disturb the stratospheric ozone layer, such as an asteroid impact, a volcanic eruption, a nuclear war, and stratospheric aerosol injection-based geoengineering.

1 Introduction

Marine phytoplankton, unicellular photosynthesizing microorganisms, are responsible for almost half of the primary production on Earth and as a result comprise the base of the marine food web (Falkowski, 2012). Phytoplankton photosynthesis and the associated drawdown of carbon dioxide are simulated in Earth system models with active ocean biogeochemistry and ecosystem components, which have been used to explore the response of global marine ecosystems to extreme events involving the injection of aerosols into the stratosphere (Lovenduski et al., 2020; Coupe et al., 2021; Harrison et al., 2022).

Photosynthesis requires light in a portion of the visible portion of the electromagnetic spectrum (400-700 nm wavelengths), i.e. photosynthetically active radiation (PAR). The relationship between phytoplankton photosynthesis and light is often represented by a photosynthesis-irradiance curve, where photosynthesis increases with light intensity until a specific threshold is reached at which point too much light can reduce phytoplankton photosynthetic capacity, also known as photoinhibition. This simplified formulation implicitly includes ultraviolet (UV, 280-400nm) inhibition, but does not consider an increasing ratio of UV radiation to PAR. At high absolute levels of UV radiation, photosynthetic apparatuses are damaged faster than repairs can be made (Cullen et al., 1992; Smith and Cullen, 1995), especially when PAR is low relative to UV. While UV inhibition of phytoplankton has been simulated in simple models (e.g., Cullen et al., 1992; Arrigo, 1994), most Earth system models do not explicitly include it.

Past work has used simple models to represent the biological effects of increased UV radiation on phytoplankton with biological weighting functions (~~BWF~~BWFs) that quantify the relative cellular damage caused by UV radiation as a function of wavelength for different phytoplankton functional types (PFTs). BWFs were determined from laboratory studies where phytoplankton cultures were exposed to varying amounts of UV radiation. Photoinhibition effects are calculated by integrating the BWF over UV wavelengths and incorporating damage by UV radiation along with photoadaptation, which may counteract UV damage. When UV-B radiation is high and PAR is low, adaptation opportunities can become overwhelmed by UV damage. While phytoplankton-specific BWFs have been implemented in simple models to capture the response to increased UV

radiation (e.g., Arrigo, 1994), no coupled Earth system models currently include representation of UV radiation inhibition in
35 marine phytoplankton. Yet, there are several potential use cases for Earth system models that incorporate UV inhibition of
phytoplankton photosynthesis.

Short-lived events that deplete stratospheric ozone, such as large asteroid impacts, volcanic eruptions, or even nuclear war,
may expose marine phytoplankton to harmful UV radiation by injecting aerosols and/or ozone depleting substances (ODS)
into the stratosphere. One of the most well known asteroid impacts caused an extinction event at the Cretaceous-Paleogene
40 boundary (K-Pg, ~66 million years ago) when the 10 km diameter Chicxulub asteroid struck the shallow sea near the present
day Yucatan Peninsula (Alvarez et al., 1980; Smit and Hertogen, 1980; Schulte et al., 2010). Soot, dust, sulfur, carbon dioxide,
water vapor, among other gases were emitted high into the atmosphere and likely caused an impact winter. While reduced
sunlight and a sudden decline in temperature (Toon et al., 2016; Bardeen et al., 2017; Henehan et al., 2019; Tabor et al.,
2020) were the ~~most-likely-main-primary~~ drivers of extinction ~~of-for~~ a significant amount of marine and terrestrial organisms
45 (Jablonski et al., 1997; Henehan et al., 2019; Tabor et al., 2020), the bombardment of the surface with UV radiation while
life ~~attempted-to-recover~~ recovered from the impact winter may have slowed the return of photosynthesizers on land and in
the ocean (Toon et al., 2016; Bardeen et al., 2017, 2021). Direct evidence of UV exposure following asteroid impacts can be
challenging to identify due to the destructive nature of the cataclysmic events that may cause such anomalies. Paleoevidence
of an increase in UV radiation contributing to an extinction event can be found in the form of malformed plant spores at the
50 Carboniferous-Devonian boundary, providing-lending some credibility to this mechanism (Marshall et al., 2020).

Model simulations allow for a quantification of ozone losses and associated increases in surface UV radiation. Simulations
of a global nuclear war support the hypothesis that surface UV radiation would increase after an injection of soot aerosols into
the stratosphere. ~~The-subsequent~~ Aerosol heating contributes to the decline of stratospheric ozone and increased surface UV-B
radiation (280 to 315 nm) in the 6 to 9 years after the war even as PAR remains below average (Bardeen et al., 2021). Similar
55 to nuclear war, asteroid impacts are likely to inject soot aerosols among dust, sulfates, and even halogens from vaporized
seawater which could deplete ozone beyond the effects of warmer stratospheric temperatures. Model simulations of asteroid
impacts over water show a decline in stratospheric ozone and increase in surface UV radiation, whether ~~considering-including~~
soot, dust, and water vapor (Bardeen et al., 2021) or just water vapor and halogens (Pierazzo et al., 2010).

Aside from past and future hypothetical extinction-level events, there are several examples in recent history of stratospheric
60 aerosol injection events disturbing the stratospheric ozone layer. Since 1970, several natural events have injected ODS into
the stratosphere and caused transient declines in stratospheric ozone. The ~~1982-eruption~~ volcanic eruptions of El Chichón ~~and~~
~~the-(1982) and Mt Pinatubo~~ (1991 ~~eruption-of-Mt.-Pinatubo-~~) released sulfur dioxide, water vapor, hydrochloric acid, and
hydrobromic acid into the atmosphere (Evan et al., 2023). After the Mt. Pinatubo eruption, ~~these-gases-caused-an-increase-in~~
~~stratospheric-sulfate-aerosols-and-local-warming-of-the-stratosphere-,the-introduction-of-sulfate-aerosols-to-the-upper-atmosphere~~
65 caused warming in the stratosphere and accelerated the heterogeneous chemical reactions that ~~contribute-to-the-destruction-of~~
~~ozone-,and-slowed-the~~ deplete ozone. Surface cooling helped slowed the vertical and poleward transport of ozone rich air from
the tropics, causing up to a 10% reduction in stratospheric ozone in the Northern Hemisphere mid-latitudes (Østerstrøm et al.,
2023). In 2021, the Hunga Tonga submarine volcano eruption ~~caused-a-5%-decline-in-stratospheric-ozone-in-the-tropics-after~~

it injected a large ~~injected sulfates and an exceptional~~ amount of water vapor ~~into the stratosphere~~ (~50 Tg) ~~in addition to~~
70 ~~sulfates into the stratosphere; a 5% decline in stratospheric ozone in the tropics followed~~ (Vömel et al., 2022; Evan et al.,
2023; Zhu et al., 2023). While most volcanic eruptions inject a plume of predominantly sulfur dioxide in the stratosphere,
~~this the~~ anomalous water vapor injection ~~demonstrated the vulnerability of stratospheric ozone to a wide variety of emissions~~
~~across a range of chemical species poses an additional risk for the ozone layer~~. Increased surface UV radiation from recent or
potential future volcanic eruptions has been studied but possible ecosystem impacts as a result ~~have not yet been studied in~~
75 ~~detail are understudied~~. Laboratory results of the estimated impact of ultraviolet radiation on phytoplankton shows there exists
the potential for the ozone loss simulated in models of these volcanic eruptions to inhibit phytoplankton growth (Cullen et al.,
1992). Similarly, the consequence of anthropogenic stratospheric aerosol emissions and its impacts on ocean ecosystems are
~~also~~ understudied.

Several "geoengineering" or climate intervention strategies have been proposed to either slow or reverse ~~global warming~~
80 ~~warming of the Earth's surface~~, but the evaluation of such actions aimed at the mitigation of climate hazards would benefit from
better understanding their potential consequences for stratospheric ozone (Stratospheric aerosol injection; MacMartin et al.,
2019; Tilmes et al., 2020). Deliberate injections of scattering aerosols into the stratosphere, which mimic the global cooling
following volcanic eruptions that release sulfur, are likely to cause stratospheric warming and increase the heterogeneous
chemical reactions that produce a depleted stratospheric ozone state (Tilmes et al., 2022). Deliberate sulfur based particle
85 injections to reduce global mean surface temperatures were found to deepen the Antarctic ozone hole within 10 years using
a high-top version of the Community Earth System Model (CESM) with interactive stratospheric chemistry (Tilmes et al.,
2021). While little is known about the biological impacts of these climate intervention strategies, we can look to the past for
an example of anthropogenic emission of an ODS that has been studied for its effects on marine ecosystems.

The multi-decadal increase in atmospheric chlorofluorocarbon (CFC) concentrations was responsible for the formation of
90 the Antarctic ozone hole (Solomon et al., 1986), which increased surface UV radiation as far north as Australia and spurred
significant scientific research into the biological effects of UV radiation. The global ban on manufacturing of CFCs via the
Montreal Protocol in 1987 halted emissions to near zero, ~~enabling the recovery~~ ~~slowing the growth~~ of the ozone hole in the
following decades (Garcia et al., 2012). Though this destruction and recovery of stratospheric ozone likely had significant bio-
logical impacts, the lack of observational studies documenting temporal trends among marine phytoplankton limits scientists'
95 ability to understand the biological response of this community as a function of changing UV irradiance (Smith and Cullen,
1995). In lieu of observational studies, lab grown phytoplankton can be exposed to varying levels of UV radiation to quantify
their sensitivity to something like an ozone hole (Cullen et al., 1992).

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. ~~As carbon dioxide emissions continue to warm~~ ~~The warming~~
100 ~~of the Earth's surface~~ ~~in regions where wind speeds do not increase may increase~~ the density gradient in the upper ocean
~~increases~~ (Li et al., 2020), resulting in increased stratification that concentrates phytoplankton in the surface layers of the ocean
where these organisms are exposed to higher amounts of harmful UV radiation (Gao et al., 2019). Mineralizing phytoplankton,
such as diatoms (silica frustules) and coccolithophores (calcium carbonate shells) rely on their shell-like structures for physical

protection, but the production of these shells may be disrupted by UV radiation (Neale et al., 1998; Lorenzo et al., 2019).
105 Coccolithophore shells, also known as coccospheres, play a role in filtering damaging UV light (Xu et al., 2016), but may
thin in response to ocean acidification (Ridgwell et al., 2009; Fox et al., 2020; Krumhardt et al., 2019). Diatom frustules offer
similar protection from UV radiation, but in contrast to coccospheres, these silica-based structures dissolve more slowly in an
acidified ocean (Aguirre et al., 2018; Taucher et al., 2022).

Numerous potential use cases motivate our development of an Earth system model capable of simulating phytoplankton
110 photosynthesis inhibition by UV radiation. Here, we describe the implementation of this new capability in the Community
Earth System Model version 2. We test the new model formulation using simulations with varying levels of UV radiation. As
we will demonstrate, UV radiation perturbs the vertical distribution of phytoplankton biomass and productivity while causing
moderate decline in global phytoplankton productivity and changes in phytoplankton community structure. Our new model
addition is a useful tool for exploring both natural and anthropogenic events that may increase marine phytoplankton exposure
115 to UV radiation.

2 Materials and Methods

2.1 Model Components

We use the Community Earth System Model version 2.1.5 (CESM2) with atmosphere, ocean, sea ice, and land compo-
nents that exchange information with each other through a coupler (Danabasoglu et al., 2020). Our ~~CESM2 code~~ modifications
120 produce a model that is capable of simulating ~~UV-B (280 to 315 nm) and UV-A (315 to 400 nm)~~ UV radiation in the atmo-
sphere, ~~propagate and propagating~~ it through the ocean, ~~and simulate UV inhibition of column, where it inhibits~~ phytoplankton
photosynthesis. We call our modified model version CESM2-UVphyto.

The atmospheric model used for this study is the Whole Atmosphere Community Climate model version 4 (WACCM4,
Marsh et al., 2013), using a grid with 1.9 x 2.5 degree horizontal resolution, 66 vertical layers and a 140 km model top.
125 WACCM4 model includes a mathematical representation of stratospheric circulation, thermodynamics, and chemistry, the last
of which is crucial for simulating UV radiation. As a "high top" model it can resolve the stratosphere in addition to parts
of the mesosphere. The Tropospheric Ultraviolet and Visible (TUV) model version 4.2 (Zerefos and Bais, 1997) is added to
WACCM4, as Bardeen et al. (2021) did, and calculates spectral integrals in-line across 100 wavelength intervals between 120
and 750 nm, instead of using a look-up table approach. Radiation between ~~280-121~~ nm and 400 nm from TUV is used to
130 compute biologically relevant parameters. The Rapid Radiative Transfer Model for GCMs (RRTMG; Iacono et al., 2000) is
used for atmospheric radiative transfer not within the UV range.

WACCM4 includes the chemistry modifications described in Bardeen et al. (2021) and a module to inject stratospheric soot
and ozone-depleting halogens, specifically hydrogen bromide and hydrogen chloride. TUV is modified to allow actinic flux to
be affected by the optical effects of aerosols. Biological weighting functions that determine UV inhibition of phytoplankton
135 photosynthesis are also incorporated into TUV (Zerefos and Bais, 1997; Bardeen et al., 2021), which also calculates surface
UV-A, UV-B, and some UV-C radiation(~~model computes spectral integrals over 121 nm to~~ UV-A radiation is between 320 nm

and 400 nm, UV-B radiation is between 280 nm ~~, compared to the defined and 320 nm, and UV-C range of radiation is defined~~
as 100 nm to 280 nm ~~)but the model is only able to compute spectral integrals from 121 to 280 nm.~~ The spectrally integrated
biological weighting functions are computed explicitly over UV-B and UV-A radiation and sent to the coupler and then to the
ocean at hourly frequency, identical to the treatment of shortwave radiation by RRTMG.

The ocean model component is the Parallel Ocean Program version 2 (POP2; Danabasoglu et al., 2020). ~~The ocean model~~
~~POP2~~ has a nominal horizontal resolution of 1 degree with 60 vertical levels, with a uniform vertical resolution of 10 m
in the upper 150 m, which increases to a maximum vertical spacing of 250 m between 3500 m and its maximum depth
of 5500 m. POP2 is coupled to an ocean biogeochemistry and ecosystem model called the Marine Biogeochemistry Library
(MARBL), which has the flexibility to resolve different plankton configurations (MARBL; Long et al., 2021). The version
of MARBL used here includes four phytoplankton functional types (PFTs), small phytoplankton, diatoms, diazotrophs, and
coccolithophores, and two zooplankton functional types (microzooplankton and mesozooplankton), a configuration referred to
as "4p2z" (Krumhardt et al., 2024). MARBL-4p2z simulates multiple nutrient co-limitation for all four PFTs.

In MARBL, small phytoplankton are limited by nitrogen, phosphorus, and iron. The small phytoplankton functional group
represents a diverse group of phytoplankton, from *Prochlorococcus* and *Synechococcus* in warm, oligotrophic regions to
groups like *Phaeocystis*, cryptophytes, and picoeukaryotes in upwelling or polar regions. ~~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.~~ Diazotrophs are nitrogen fixing bacteria
that are limited by phosphorus and iron. Diatoms are silicifiers that are limited by nitrogen, phosphorus, iron, and are the only
PFT limited by silicon. Coccolithophores are limited by nitrogen, phosphorus, iron, and are the only PFT limited by carbon.
The coccolithophore PFT is primarily represented as *Emiliana huxleyi* in MARBL-4p2z, based on Krumhardt et al.
(2019), and simulates calcium carbonate production as a function of temperature, aqueous CO₂, and phosphorus limitation.
~~In total, the dynamics of four morphotypes of Emiliana huxleyi, as well as other species such as Calcidiscus leptoporus and~~
~~Gephyrocapsa ozeanica were used to construct the PFT, allowing the model to simulate the general response of coccolithophores~~
~~to environmental changes Krumhardt et al. (2019).~~ Microzooplankton graze on phytoplankton, while mesozooplankton graze
on both phytoplankton and microzooplankton. Other than grazing, loss of phytoplankton can occur through aggregation and
subsequent sinking through the column. ~~We also performed UV sensitivity simulations using two other configurations of~~
~~MARBL: "4p1z" (4 phytoplankton and only 1 zooplankton), and "3p1z" (3 phytoplankton and 1 zooplankton). In the 3p1z~~
~~configuration, coccolithophores are not represented but an implicit calcifier is included as a changing percentage of the small~~
~~phytoplankton PFT.~~

Phytoplankton photosynthesis in all MARBL configurations is calculated by scaling the maximum growth rate by limita-
tion functions for temperature, light, and nutrient availability (Long et al., 2021). Phytoplankton photosynthesis increases in
response to increasing PAR, following the light limitation formulation from Geider et al. (1998). Photoadaptation is repre-
sented as a varying chlorophyll to carbon ratio for each PFT, depending on light, temperature, and nutrient limitations (Geider
et al., 1998). PAR in MARBL is estimated as 45% of surface shortwave radiation and is attenuated with depth as a func-
tion of chlorophyll concentration, taking into consideration shading by phytoplankton. Zooplankton are not considered in the

light attenuation equation, as they do not contain chlorophyll and do not absorb light as effectively as phytoplankton. In high concentrations, zooplankton may impact light attenuation, but these populations tend to overlap with high phytoplankton concentrations which already significantly attenuate light. In CESM2-UVphyto, phytoplankton growth rates can be slowed by increased UV radiation, as described in Section 2.2. While TUV provides a direct calculation of PAR, the simulations here use the PAR estimation from shortwave radiation in order to test the sensitivity of the model to the new UV radiation scheme alone.

Source code modifications to WACCM4, TUV, POP2, and MARBL were required to enable the calculation of UV inhibition. In WACCM4, this includes the integration of TUV and modules used to simulate aerosol injections relevant for asteroid impacts (Bardeen et al., 2017, 2021). New BWFs relevant for the phytoplankton species simulated in MARBL were added to TUV. Modifications to the CESM2 model coupler were made to pass UV radiation fields to POP2, and POP2 was modified to pass information to MARBL, where UV inhibition of photosynthesis is calculated. All other components are used without modification from the cesm2.1.5 ~~code base~~.

The sea ice model is CICE5 with interactive sea ice that shares the same horizontal grid as ~~the ocean model~~ POP2 (Hunke et al., 2015). CICE5 includes mushy-layer thermodynamics and a melt pond parameterization that produces melt ponds preferentially on undeformed sea ice. Sea ice is allowed to affect PAR attenuation with depth in the ocean model using a subgrid-scale sea ice thickness distribution (Long et al., 2015). Essentially, various sea ice thickness categories can impact the ability of phytoplankton to grow underneath sea ice. In CESM2-UVphyto, UV radiation interaction with sea ice is identical to the treatment of shortwave radiation, until UV radiation reaches the water, at which point its attenuation accelerates rapidly compared to PAR.

The land model is the Community Land Model version 5 (CLM5) with a carbon-nitrogen cycle (Lawrence et al., 2019). It simulates the evolution of the land physical state, characteristics of the land surface, exchanges of energy and material with the atmosphere, and run-off into the ocean. CLM5 has a horizontal resolution of 1.9 x 2.5 degrees which is shared with the atmosphere grid, with 15 vertical layers for the land and 10 vertical layers for lakes. Photosynthesis of terrestrial vegetation is not inhibited by UV radiation, but future work is expected to incorporate this functionality.

2.2 Calculation of Ultraviolet Inhibition of Photosynthesis

Biological weighting functions (BWF) for UV inhibition for each PFT (see Section 2.3) are integrated over the UV-A ~~and~~ UV-B portion, and UV-C portions of the electromagnetic spectrum in TUV and used to calculate surface E_{inh}^* , a biologically weighted dimensionless UV dosage rate, according to Cullen et al. (1992),

$$E_{inh}^* = \sum_{\lambda=280nm}^{\lambda=200nm} E(\lambda) \cdot \epsilon(\lambda) \cdot \Delta\lambda, \quad (1)$$

where $E(\lambda)$ is the surface spectral irradiance at wavelength λ , and $\epsilon(\lambda)$ is the BWF $((mW m^2)^{-1})$ representing the inhibition of photosynthesis by UV radiation. λ spans the UV spectrum of radiation from 121 nm to 400 nm and is subdivided into UV-A, UV-B, and UV-C components. E_{inh}^* can be thought of as the total integrated potential damage phytoplank-

ton will suffer from ~~aeross~~-radiation in the UV spectrum. While some laboratory studies include a PAR inhibition term in
 205 E_{inh}^* (Neale and Thomas, 2016), our model configuration does not account for this term; in our simulations, high UV is not
accompanied by high PAR. The BWF, given by $\epsilon(\lambda)$, describes how each wavelength interval contributes to that damage.
 E_{inh}^* values are determined at every surface model grid cell and time step for small phytoplankton, diatoms, diazotrophs, and
 coccolithophores.

E_{inh}^* is passed from the atmospheric model (TUV) to the marine biogeochemistry model (MARBL) and propagated ver-
 210 tically through the water column. To capture the rapid attenuation of UV radiation with depth in the ocean, we compute
 E_{inh}^* at a given model level using the ~~equation in Overmans and Agustí (2020), which relates depth profiles of chlorophyll~~
~~concentration and relationship between chlorophyll and the attenuation coefficient (K_{dUV}) in Tedetti et al. (2007).~~ Because
attenuation varies as a function of wavelength, E_{inh}^* is subdivided into UV-A, UV-B radiation ($\lambda = 305$ nm) for oligotrophic
ocean conditions:-

215 $K_{d-UV} = 0.14 \cdot \text{CHL} + 0.29,$

, and UV-C components before being passed to the ocean. The attenuation coefficient, K_{dUV} has three forms: K_{dUV-A} ,
 K_{dUV-B} , or K_{dUV-C} , calculated using the following relationships where the attenuation coefficient ~~, K_{d-UV} ,~~ is computed
 as a function of chlorophyll (CHL, mg m^{-3}). ~~This equation:-~~

$K_{dUV-A} = 0.24 \cdot \text{CHL} + 0.04,$ (2)

220

$K_{dUV-B} = 0.44 \cdot \text{CHL} + 0.13,$ (3)

$K_{dUV-C} = 0.60 \cdot \text{CHL} + 0.40,$ (4)

This is based on an equation that was determined empirically ~~using stationary radiometers collecting spectrally integrated~~
 225 ~~UV-B (280 to 315 nm) and UV-A (315 to 400 nm) radiation over 10 minute intervals along coral reefs in the Red Sea~~
~~and measurements of chlorophyll-a using a Trilogy Fluorometer (Overmans and Agustí, 2020) under open ocean conditions~~
(Tedetti et al., 2007). E_{inh}^* is propagated through the column as a function of K_{d-UV} and the thickness of a particular model
 layer, dz (m):

$E_{inh}^*(k+1) = E_{inh}^*(k) \cdot \exp(-K_{d-UV} \cdot dz),$ (5)

230 where k is the vertical layer index. According to this relationship, for chlorophyll concentrations of 0.02 mg m^{-3} (the mini-
 mum value used for calculating the impact of chlorophyll on the vertical propagation of PAR in MARBL), the depth at which

UV-B radiation declines to 1% of the surface value ($Z_{1\%}$) is $\sim 16-33$ m. At higher chlorophyll concentrations ($\sim 0.85 \text{ mg m}^{-3}$, approximately the highest peak found in Overmans and Agustí (2020)) the depth at which surface UV radiation attenuates to 1% ($Z_{1\%}$ for UV-B radiation is ~ 9 m depth, effectively restricting UV inhibition to the first model level. In the clearest waters possible, $Z_{1\%}$ of UV-C radiation is 11 m, while at chlorophyll concentrations of 0.85 mg m^{-3} , $Z_{1\%}$ for UV-C radiation is approximately 5 m, or the midpoint of the first model level. UV-A radiation propagates to ~ 98 m depth before reaching $Z_{1\%}$ under the clearest waters, indicating greater potential for UV-A damage than for UV-B and UV-C.

UV inhibition of photosynthesis in CESM2-UVphyto primarily occurs in the upper 20 m of the water column and depends greatly on shading by phytoplankton. Because POP has upper layers that are 10 m thick, it is only the top two layers of the ocean that experience UV inhibition. We use the mid-point of the layer to calculate attenuation for each layer, which may underestimate the influence of much higher E_{inh}^* within the top 5 m of the level, but could overestimate E_{inh}^* within the bottom 5 m of the level. The effect of ocean surface roughness from waves on UV radiation entering the surface ocean is not considered in the attenuation of UV radiation.

Finally, a UV inhibition term (γ_{UV}) is computed at every model level, similar to nutrient and light limitation, using γ_{UV} is computed using three different functional forms or “models”, depending on the functional form from Arrigo (1994):

$$\gamma_{UV} = \frac{1}{1 + E_{inh}^*},$$

where used to derive the biological weighting functions (Table 1). These include the “E” model, the “T” model, and the “Emax” model, which relate E_{inh}^* to γ_{UV} . γ_{UV} ranges from 0 (total UV inhibition) to 1 (no UV inhibition) and is included in the calculation of the growth rate for phytoplankton from Long et al. (2021),

$$\mu_i = \mu_{max}(T) \cdot \gamma_N \cdot \gamma_l \cdot \gamma_{UV}, \quad (6)$$

where μ_i represents the growth rate of a particular PFT, $\mu_{max}(T)$ represents the maximum growth rate at a given temperature, and γ_N and γ_l represent nutrient and light limitation terms, respectively, ranging from 0 (no nutrients/light) to 1 (sufficient nutrients/light). In this way the γ limitation terms reduce the maximum growth rate multiplicatively.

2.3 Determination of Biological Weighting Functions

The expansion of the Southern Hemisphere ozone hole during the 1980s due to the emission of chlorofluorocarbons in the decades prior prompted studies into the susceptibility of marine life and phytoplankton to UV radiation. These efforts produced biological weighting functions (BWFs) specific to different PFTs that are suitable for the simulation of UV inhibition in of photosynthesis. We utilized both laboratory and *in-situ* studies with appropriate BWFs for the phytoplankton community represented within MARBL (Figure 1). For diatoms, we used the BWF based on the E model reported in Cullen et al. (1992), who measured changes in productivity of the diatom *Phaeodactylum sp.* by exposing samples of the species to a range of

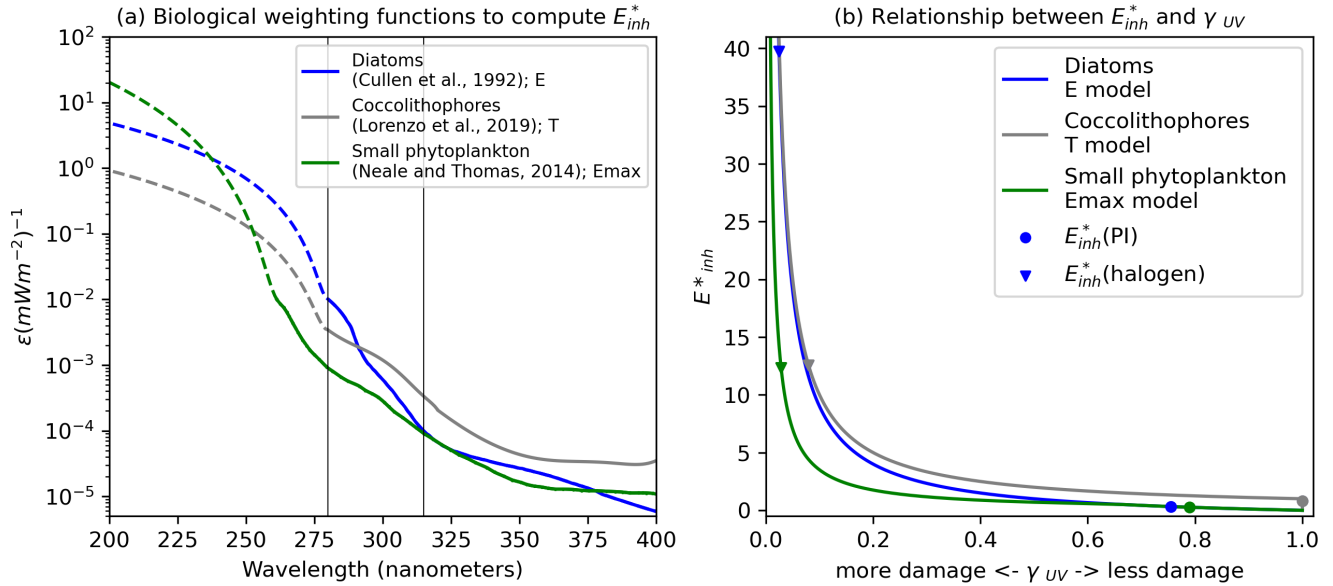


Figure 1. (a) Species-specific biological weighting functions showing the biological efficiency for ~~damage-to-inhibition of~~ phytoplankton photosynthesis by ultraviolet light as a function of wavelength. Depicted here are the weighting functions for diatoms (Cullen et al., 1992), coccolithophores (Lorenzo et al., 2019), small phytoplankton and diazotrophs (Neale and Thomas, 2016) (Neale et al., 2014) that were used in our simulations of CESM2-UV. ~~Black line represents~~ Dashed lines indicate extrapolated values and the division between UV-A vertical black lines are the divisions of UV-C/UV-B and UV-B/UV-A radiation from left to right. (b) Relationship between E_{inh}^* and γ_{UV} for the different phytoplankton functional types and models and under different UV conditions.

wavelengths of UV and PAR. ~~A look-up table is provided in Supplemental Table 1. Wavelengths were~~ Look-up tables are provided as csv files in *Model code and software* for the three BWFs shown in Figure 1a. Wavelengths are interpolated to the bounds provided in this table to calculate spectral integrals. Diatoms show relatively low sensitivity to UV-A light, but are exponentially more sensitive to UV-B light, especially for wavelengths shorter than 290 nm.

265 For coccolithophores, ~~which are designed to represent the species *Emiliana huxleyi* in MARBL, we adopted the BWF reported by Lorenzo et al. (2019)—a 6th order polynomial that separately computes $\epsilon(\lambda)$ for UV-B and UV-A wavelengths in for a heavily calcified species of *Emiliana huxleyi* by Lorenzo et al. (2019) which was constructed using the T model (see Table 1. Lorenzo et al. (2019) used similar methods for determining sensitivity to UV radiation as Cullen et al. (1992), but also explored how elevated atmospheric CO₂ concentrations impacted the sensitivity of coccolithophore photosynthesis to UV~~

270 ~~radiation. At elevated CO₂ concentrations, *Emiliana huxleyi* cells exhibit decreased rates of calcification (Lorenzo et al., 2019). Affected cells may be able to reallocate energy towards producing organic material despite difficulties in forming calcium carbonate shell material. Some work has suggested that thinner coccospheres will allow more UV radiation to penetrate into the cell, making the cell). The T model permits no UV limitation until E_{inh}^* reaches 1, at which point damage is more sensitive to changes in radiation than in the E model. Because laboratory experiments have revealed that the thinning of coccolithophore~~

275 shells may make them more susceptible to photoinhibition (Guan and Gao, 2010). This sensitivity is explored in UV damage
(e.g. Guan and Gao, 2010), our model includes an optional feature that enhances UV damage when environmental conditions
result in thinned coccolithophore shells (thickness determined by the PIC/POC ratio; see Section 2.4).

We use the *Synechococcus* BWF reported in Neale and Thomas (2016) Neale et al. (2014) for both small phytoplankton and
diazotrophs. Neale et al. (2014) and Neale and Thomas (2016) studied UV sensitivity of *Prochlorococcus* and *Synechococ-*
280 *cus* from temperate and tropical open-ocean regions under different UV exposures and water temperatures. The BWF from
Neale and Thomas (2016) for *Synechococcus* from Neale et al. (2014) most closely resembles the species for small phytoplankton
in MARBL and is based on a 7-28% decline in productivity due to enhanced UV radiation in a laboratory study that the small
phytoplankton functional group in MARBL is intended to represent. This BWF is constructed using the Emax model, which
is equivalent to the E model until E_{inh}^* surpasses 0.54, at which point UV damage increases as a much faster rate as E_{inh}^*
285 increases.

The effects of UV radiation on diazotrophs has have been examined to some extent (Lesser, 2008; Cai et al., 2017), but none
have reported usable BWFs for computing UV damage as a function of wavelength. Lesser (2008) found that diazotrophs were
quite sensitive to UV radiation, while Cai et al. (2017) found that UV-absorbing compounds in high-light grown diazotrophs
(*Trichodesmium*) can mitigate some but not all UV damage. The shallow depth of *Trichodesmium* coupled with its importance
290 of supplying nitrogen to oligotrophic gyre ecosystems suggests a potentially important regional role for UV inhibition of
nitrogen fixers. We generalize diazotrophs by using the same BWF as reported by Neale and Thomas (2016) Neale et al. (2014),
therefore representing a mid-point between the BWFs for the diatoms and coccolithophores. A 6th order polynomial to compute
 $\epsilon(\lambda)$ for all UV wavelengths for small phytoplankton and diazotrophs is provided in Table 1. Diazotrophs lack mineral shells
like diatoms and coccolithophores, and thus are more akin to small phytoplankton in their sensitivity to UV. Diazotrophs
295 comprise less than 3% of global phytoplankton net primary productivity in pre-industrial MARBL-3p1z simulations, meaning
large uncertainties in how diazotrophs will respond to UV radiation do not significantly affect global productivity or nutrient
cycling over shorter (decadal) timescales but may have regional impacts that CESM2-UVphyto can consider.

Not all of the employed BWFs extend into wavelengths below 280 nm (UV-C radiation). While UV-C radiation is a
non-factor even under a relatively depleted ozone layer, it may become relevant after a cataclysmic asteroid impact. We account
300 for potential UV-C radiation damage by extrapolating the BWFs to wavelengths of 200 nm (dashed lines in Figure 1a).

2.4 Scaling UV inhibition of coccolithophore photosynthesis as a function of shell thickness

Coccolithophores construct shells out of calcium carbonate, providing protection from grazing, viral attacks, as well as from
harmful amounts of PAR and UV radiation (Monteiro et al., 2016; Krumhardt et al., 2019; Xu et al., 2016; Lorenzo et al.,
2019). In MARBL, coccolithophores have the lowest maximum grazing rate, partly because of the protection from their shell.
305 Laboratory studies of calcified and thin-shelled, or "naked" coccolithophores have found that the shell reduces the
transmission of UV-B radiation by 18% (Xu et al., 2016). In response to decreased transmission of UV-B, calcified cells in
outdoor conditions were also found to have 3.5 times higher growth rates than "naked" coccolithophores (Xu et al., 2016).

Table 1. Different phytoplankton functional types (PFTs) and the study that determined the specific biological weighting functions (BWFs) we used in simulations of CESM2-UVphyto. Units are in $(\text{mW m}^{-2})^{-1}$.

Phytoplankton	Study	Biological-Weighting-Functions <u>Equation</u>
Siliceous Diatoms	Cullen et al. (1992)	Provided in look-up table (see Table S1). <u>E model</u> $\gamma_{UV} = \frac{1}{1 + E_{inh}^*}, \quad (7)$
Calcifying Coccolithophores	Lorenzo et al. (2019)	 $\epsilon(\lambda) \text{ for UV-B} = (-1.40530706 \times 10^{-12})\lambda^6 + (2.39353416 \times 10^{-9})\lambda^5 + (1.68928198 \times 10^{-6})\lambda^4 + (6.31865068 \times 10^{-4})\lambda^3 - 0.131975456\lambda^2 + 14.5753274\lambda - 663.797953$ <u>T model</u> $\gamma_{UV} = 1, E_{inh}^* < 1 \quad (8)$ $\gamma_{UV} = \frac{1}{E_{inh}^*}, E_{inh}^* \geq 1 \quad (9)$ $\epsilon(\lambda) \text{ for UV-A} = (8.89581784 \times 10^{-15})\lambda^6 - (1.93953328 \times 10^{-11})\lambda^5 + (1.76199028 \times 10^{-8})\lambda^4 - (8.53798419 \times 10^{-6})\lambda^3 + 0.00232766669\lambda^2 - 0.338550975\lambda + 20.5261692$
Small phyto- plankton and Diazotrophs	Neale and Thomas (2017 <u>2014</u>)	<u>E_{max} model</u> $\gamma_{UV} = \frac{1}{1 + E_{inh}^*}, E_{inh}^* \leq E_{max}^* \quad (10)$ $\gamma_{UV} = \frac{1}{C * E_{inh}^*}, E_{inh}^* > E_{max}^* \quad (11)$ $c = \frac{1 + E_{max}^*}{E_{max}^*}; \quad (12)$ $E_{max}^* = 0.54 \quad (13)$ $\epsilon(\lambda) = (-3.10572006 \times 10^{-15})\lambda^6 + (6.27284524 \times 10^{-12})\lambda^5 - (5.22236845 \times 10^{-9})\lambda^4 + (2.28848111 \times 10^{-6})\lambda^3 - (5.54843743 \times 10^{-4})\lambda^2 + 0.0702209062\lambda - 3.59639531$

When UV was removed in indoor conditions, growth rates were still 2 times higher than in outdoor conditions, indicating a growth enhancement of 1.75 times when UV is not present.

310 In CESM2-UVphyto, coccolithophore shell thickness is related to the instantaneous ratio of particulate inorganic carbon (PIC; calcium carbonate) to particulate organic carbon (POC), $\frac{PIC}{POC}$ (Krumhardt et al., 2019). Shelled coccolithophores have a $\frac{PIC}{POC} > 0.05$, while ‘naked’ coccolithophores have a $\frac{PIC}{POC} \leq 0.05$. In CESM2, PIC/POC is also influenced by the aqueous CO₂ concentration, such that elevated CO₂ corresponds with lower PIC/POC values (Krumhardt et al., 2019). To accommodate the UV inhibition of coccolithophore photosynthesis that accompanies thinning coccolithophore shells, we have included
 315 a PIC/POC scaling option that can be toggled on and off, where we modify γ_{UV} when ~~sufficient UV radiation is present~~ $(E_{inh}^* > 0.5)$ a minimum level of UV damage is reached ($E_{inh}^* > 0.25$) as follows:

$$\gamma_{UV}(\text{shelled}) = \underline{CS} \cdot \gamma_{UV}(\text{naked}), \quad (14)$$

where

$$\underline{CS} = \begin{cases} 1.75^{-1}, & \text{if } \frac{PIC}{POC} < 0.05, \\ \left(\frac{PIC}{POC}\right)^{\frac{1}{6}}, & \text{otherwise.} \end{cases} \quad (15)$$

320 Our γ_{UV} scaling aligns with the Xu et al. (2016) finding that calcified cells have growth rates 3.5 times higher than naked shells under moderate levels of UV radiation. ~~Results from simulations without PIC/POC scaling of UV inhibition to coccolithophores are shown in the Supplemental Information document~~ As CESM2-UVphyto does not have explicit PAR inhibition, we adjust the scaling factor downwards to 1.75.

2.5 Pre-industrial simulations with low UV radiation

325 We conduct two simulations with CESM2-UVphyto under no or low levels of UV radiation to ensure that our new BWFs do not disrupt the normal functioning of the biogeochemical and ecosystem model. Both of these test simulations use the 4p2z configuration of MARBL and pre-industrial atmospheric forcing consistent with the year 1850 and atmospheric CO₂ concentration set to 284.7 ppm. The first is a 10-year coupled simulation of CESM2-UVphyto with an E_{inh}^* value of zero that branches from a previously spun-up ocean physical and biogeochemical state ~~Krumhardt et al. (2024)~~ (Krumhardt et al., 2024);
 330 the UV forcing from this simulation is referred to as $E_{inh}^*(0)$. The end of the $E_{inh}^*(0)$ simulation is used as the initial condition for all subsequent simulations. The second simulation probes the impact of the new BWFs on the resulting biogeochemical state under 5 years of pre-industrial (*i.e.*, low) UV radiation levels, $E_{inh}^*(PI)$. This simulation of ocean biogeochemical sensitivity to pre-industrial levels of UV radiation (and subsequent ones) are conducted in ocean-ice only mode, *i.e.*, a simulation of CESM2-UVphyto with only the ocean and ice component models that is forced by saved surface states and fluxes from coupler
 335 output files; UV-A, UV-B, and UV-C radiation; and E_{inh}^* for each BWF at the air-sea interface. These forcings are derived from a year-long, fully coupled simulation of CESM2-UVphyto with WACCM4 coupled to TUV under pre-industrial levels

of UV radiation, and produce a global average annual mean surface E_{inh}^* (diatoms) of ~~0.34~~0.32, E_{inh}^* (small phytoplankton & diazotrophs) of ~~0.71~~0.82, and E_{inh}^* (coccolithophores) of ~~0.74~~0.27. Because of the lack of ODS in the pre-industrial stratosphere, UV radiation is elevated in the present day compared to the pre-industrial in terms of UV index by up to 13% in tropical regions, 10% in the Antarctic, and 4% in Arctic regions. However, the surface UV radiation levels present in these simulations are well within the range of those used in laboratory studies that informed the construction of BWFs. ~~We note that while a single year of forcing does not capture interannual variability and could potentially be anomalous, we see below that the results from the forced $E_{inh}^*(PI)$ simulation are indistinguishable from the coupled $E_{inh}^*(0)$ simulation.~~

2.6 Pre-industrial simulations with elevated UV radiation

We conduct 5 year simulations to explore the modeled biogeochemical and ecological response to ~~extremely~~ high levels of surface UV radiation. ~~In a case referred to as $E_{inh}^*(20\times PI)$, forcings at the air-sea interface are derived from previously described year-long, fully coupled simulation of CESM2-UVphyto with WACCM4-TUV, except for E_{inh}^* . $E_{inh}^*(20\times PI)$ uses coupler fluxes from the $E_{inh}^*(PI)$ simulation with only E_{inh}^* increased by a factor of 20 for all PFTs. This value is approximately the average E_{inh}^* response for a large injection of soot, hydrogen bromide and hydrogen chloride into the stratosphere, destroying 95% of all stratospheric ozone globally. This UV forcing is not intended to perfectly simulate an asteroid impact, but represents an~~ Halogens equivalent to emissions from the Chicxulub asteroid impact at the K-Pg boundary Toon et al. (2016) are injected into the stratosphere. The halogen injection includes 117,000 Tg hydrogen chloride and hydrogen bromide and is intended to mimic an upper bound of a possible surface UV radiation ~~to test the upper range of the selected BWFs. The perturbation without affecting visible light. Global atmospheric circulation is affected by the depletion of stratospheric ozone, but there are~~ minimal changes to the surface radiative budget. This case is referred to as $E_{inh}^*(\text{halogen})$. A fully coupled simulation is run for ~~five years, or five cycles of the year-long saved forcing~~ two years and coupler forcing is used to generate a five-year offline simulation; for simplicity, the forcing from the second year of the fully coupled simulation is repeated for 4 years for the offline simulation.

2.7 Elevated CO₂ simulations

At higher atmospheric CO₂ concentrations, coccolithophores in some regions may experience a carbon fertilization effect as carbon used for photosynthesis become less limiting, allowing for faster growth compared to lower CO₂ concentrations (Krumhardt et al., 2017, 2019). However, coccolithophores' ability to construct and maintain thick calcium carbonate shells (i.e., high PIC/POC ratios) may be inhibited (Krumhardt et al., 2019). To explore UV inhibition in conditions that engender thinner coccolithophore shells, we conducted a range of ocean and sea-ice only simulations with varying atmospheric CO₂ concentrations at the ocean's surface: 284 ppm, 400 ppm, 600 ppm, 700 ppm, and 900 ppm. First, these simulations are spun-up with no UV radiation inhibition ($E_{inh}^*(0)$) and CO₂= 284.7 ppm until the ~~upper ocean mixed layer~~ (0-100m) global average pH exhibits little change with time, occurring after 15 years of simulation. The simulation with CO₂= 400 ppm uses the end of the CO₂ = 284 ppm simulation as an initial condition, the end of the simulation with CO₂= 400 ppm is used as the initial condition for the ~~CO₂=600 ppm~~ simulation, the end of the simulation with CO₂=600 ppm is used to start ~~the CO₂=700~~ the 700

370 ppm simulation, and the end of the simulation with CO₂=700 ppm is used to start the CO₂=900 ppm simulation. This approach speeds up the spin-up as atmospheric CO₂ concentrations progress higher. All simulations with CO₂ levels greater than 284.7 ppm are run for 17 years, at which point variations in upper ocean global average pH are smaller than 0.01 from year to year. Next, $E_{inh}^*(PI)$ is imposed for 1 year starting at the end of each simulation with incrementally increasing atmospheric CO₂ (400 ppm, 600 ppm, 700 ppm, 900 ppm). Finally, $E_{inh}^*(20\times PI_{halogen})$ is imposed for 1 year in the same manner as $E_{inh}^*(PI)$ 375 , using the same initial condition. [Detailed information about each simulation can be found in Table S1.](#)

3 Results

UV radiation at the ocean's surface causes a reduction in globally integrated phytoplankton net primary productivity (NPP) through inhibition of photosynthesis in the top 20-40 m of the ocean under $E_{inh}^*(PI)$ and $E_{inh}^*(20\times PI_{halogen})$ forcing. Under the control $E_{inh}^*(0)$ forcing, annual-mean globally integrated top 150 m NPP equilibrates to 55 Pg C yr⁻¹ in the 4p2z 380 configuration, which is well within the range of satellite estimates (43-67 Pg C yr⁻¹ ; Behrenfeld and Falkowski, 1997 and Behrenfeld et al., 2006) and similar to other configurations of MARBL ([see Supplemental Information: Phytoplankton Validation](#))([Long et al., 2021](#)). Under $E_{inh}^*(PI)$ UV forcing, annual-mean global NPP is reduced by 15.4% compared to $E_{inh}^*(0)$, as shown in Figure 2a. ~~Our findings are consistent with the hypothesis that~~ [The results indicate a statistically significant change in global NPP under pre-industrial UV radiation should not significantly impact globally integrated NPP compared to simulations without UV radiation.](#) In the $E_{inh}^*(20\times PI_{halogen})$ case, annual-mean globally integrated NPP declines by 7.5% to 385 50.8-6.5% to 51.9 Pg C yr⁻¹ compared to the $E_{inh}^*(0)$ simulation (Figure 2a). ~~The global NPP response to larger UV forcing in the Under $E_{inh}^*(20\times PI)$ case is within the very large range of anticipated response of phytoplankton to UV inhibition in the context of increased UV radiation under the Southern Hemisphere ozone hole(see Supplemental Information: Phytoplankton Under Ozone Hole Stress)~~ [halogen\), stratospheric ozone declines by more than 90%, producing UV indices greater than 30 over the Antarctic, exceeding the greatest values of up to 14 over Antarctica under the ozone hole.](#) 390

The phytoplankton productivity response to UV inhibition is a function of characteristics unique to each phytoplankton type, with some types ~~showing increases in productivity benefiting~~ at the expense of others. Small phytoplankton constitute half of the [annual mean](#) globally integrated NPP in both the $E_{inh}^*(0)$ and $E_{inh}^*(PI)$ simulations (Figure 2b), while diatoms contribute approximately 40%. ~~Both Together, both~~ [coccolithophores and diazotrophs combined make up contribute](#) around 395 10% [to global NPP](#). Under preindustrial levels of UV radiation (case $E_{inh}^*(PI)$), the relative contribution of each PFT to global NPP is virtually unchanged and the timing of seasonal blooms are not significantly altered when compared to the $E_{inh}^*(0)$ case (Figure 2b). Under $E_{inh}^*(20\times PI_{halogen})$ forcing, diatom productivity ~~increases,~~ and small phytoplankton productivity ~~decreases relative changes are inversely related~~ (Figure 2b). [Relative to the \$E_{inh}^*\(0\)\$ case, diatoms perform better during April, November, December, and January](#) (Figure 2b). During the month of April, small phytoplankton shift from comprising a clear 400 majority of global phytoplankton NPP to generating nearly the same global productivity as diatoms in the $E_{inh}^*(20\times PI_{halogen})$ case (Figure 2b). The relative contribution of diazotrophs to global total NPP is not modified with UV radiation (Figure 2b).

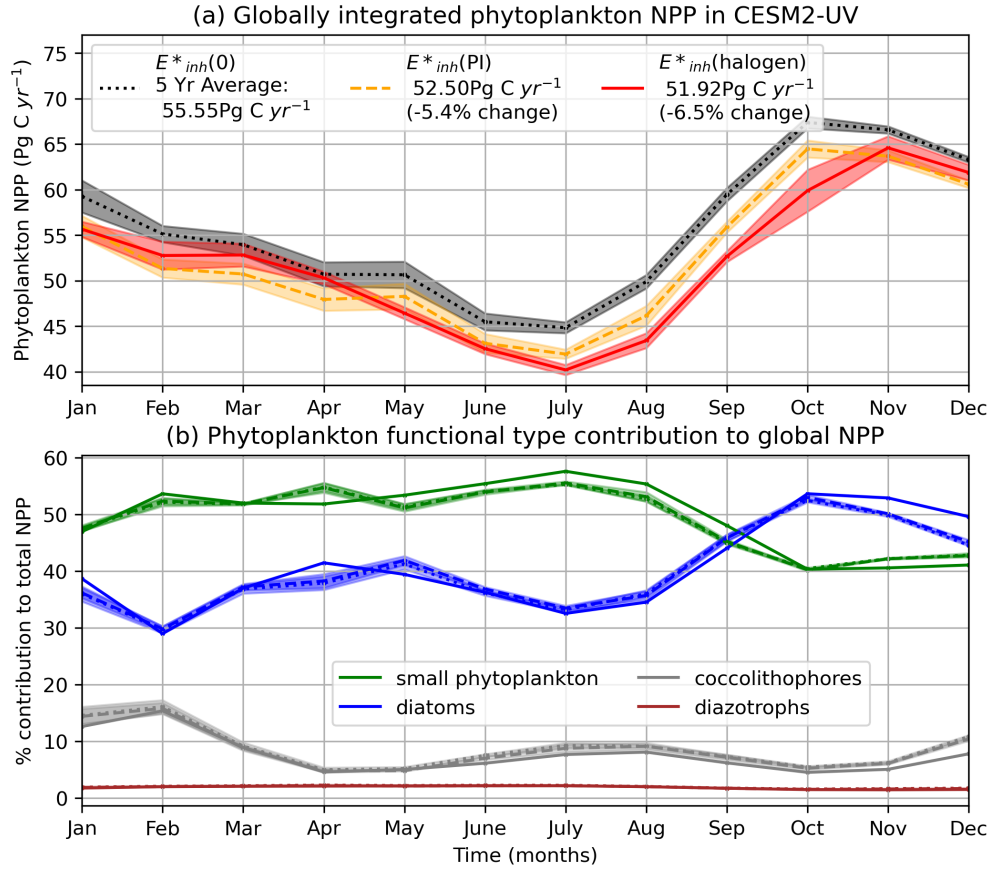


Figure 2. (a) Globally integrated 5-year mean monthly NPP climatology integrated over the top 150 m (Pg C yr⁻¹) in the $E_{inh}^*(0)$, $E_{inh}^*(PI)$, and $E_{inh}^*(20\times PI\ halogen)$ simulations. Shading indicates 1 standard deviation below and above the 5-year mean for each month. (b) Each phytoplankton functional type's % contribution to globally-integrated NPP in the (solid) $E_{inh}^*(20\times PI\ halogen)$, (dashed) $E_{inh}^*(PI)$, and (dotted) $E_{inh}^*(0)$ simulations. Note the $E_{inh}^*(PI)$ and $E_{inh}^*(0)$ simulations are nearly indistinguishable.

Enhanced UV radiation b). $E_{inh}^*(halogen)$ forcing reduces the contribution of coccolithophore productivity to global NPP from December to February.

The relative responses of phytoplankton NPP to UV radiation across the different PFTs are driven primarily by the BWFs of the different PFTs (Figure 1) which generate E_{inh}^* (Figure 3). In the $E_{inh}^*(PI)$ simulation, coccolithophore UV damage (E_{inh}^*) is the largest of all the PFTs in all months of the year, followed by small phytoplankton/diazotroph and then diatom damage (PI forcing) (Figure 3a). This finding is consistent with the relative UV damage (E_{inh}^*) across the PFTs in the $E_{inh}^*(PI)$ simulation (Figure 3a), even though the weighting functions of the PFTs exhibit different responses to UV radiation as a function of wavelength (Figure 1). One could imagine conducting a simulation with CESM2-UV phyto forced by a large aerosol injection that depletes stratospheric ozone in ways that non-linearly

Annual mean γ_{UV} for all PFTs

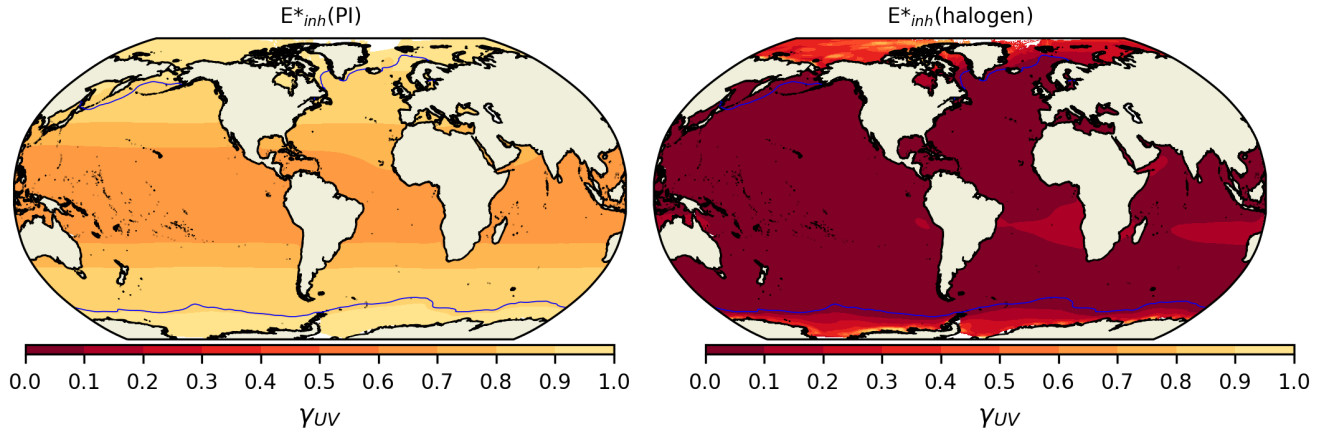


Figure 3. (a) Global average E_{inh}^* for each PFT for both $E_{inh}^*(PI)$ (dashed) and $E_{inh}^*(20\times PI)$ (solid). (b) The spatial distribution of total average E_{inh}^* surface γ_{UV} for all PFTs under (left) $E_{inh}^*(PI)$ and (right) $E_{inh}^*(20\times PI)$ over five years of simulation, weighted by the distribution of each PFT. Maximum annual sea ice extent is indicated by the blue solid line. Higher-Lower values of $E_{inh}^*\gamma_{UV}$ indicate greater plankton limitation.

increase UV-B radiation at wavelengths between 280 and 290 nm, for which diatom UV damage would be larger than those of the other PFTs (see, e.g., Figure 1), which would produce a very different NPP response. (halogen) simulation, small phytoplankton have the most damaging γ_{UV} . The net impact of UV radiation on phytoplankton NPP in CESM2-UVphyto is further determined by the latitude and depth at which the majority of the population of each PFT resides. For example, the

415 highest E_{inh}^* values can be found at the lowest latitudes (Figure 3a) and small phytoplankton exist in greatest numbers at low latitudes, indicating high vulnerability relative to the other phytoplankton types. Under preindustrial levels of UV radiation (case $E_{inh}^*(PI)$), the spatial distribution of phytoplankton productivity for each PFT (Figure 4a) is similar to the distributions reported in Long et al. (2021) using a MARBL-3p1z configuration that resolves these functional types. Coccolithophore NPP (Figure 4a) and their $CaCO_3$ production (not shown) share a similar spatial pattern with that shares broad similarities to patterns

420 reported in Krumhardt et al. (2019) using a MARBL-4p1z configuration that includes coccolithophores. The addition of a second zooplankton class reduces excessive $CaCO_3$ production in large blooms present in the MARBL-4p1z configuration. Relative to a case with no UV radiation ($E_{inh}^*(0)$), small phytoplankton and diazotrophs experience declines in NPP in the tropical and subtropical regions, where they have higher biomass under normal conditions relative to other regions; small phytoplankton have increased NPP in the subpolar regions, at the expense of coccolithophore NPP, indicating that decreased

425 fitness of coccolithophores in the regions where they are most abundant is opening up creates habitat for small phytoplankton productivity under UV stress (Figure 4b).

While E_{inh}^* and its change with UV radiation is approximately zonally homogeneous (Figure 3b), the response of phytoplankton NPP to enhanced UV radiation in the $E_{inh}^*(20\times PI)$ case is zonally heterogeneous, especially for diatoms and coccolithophores

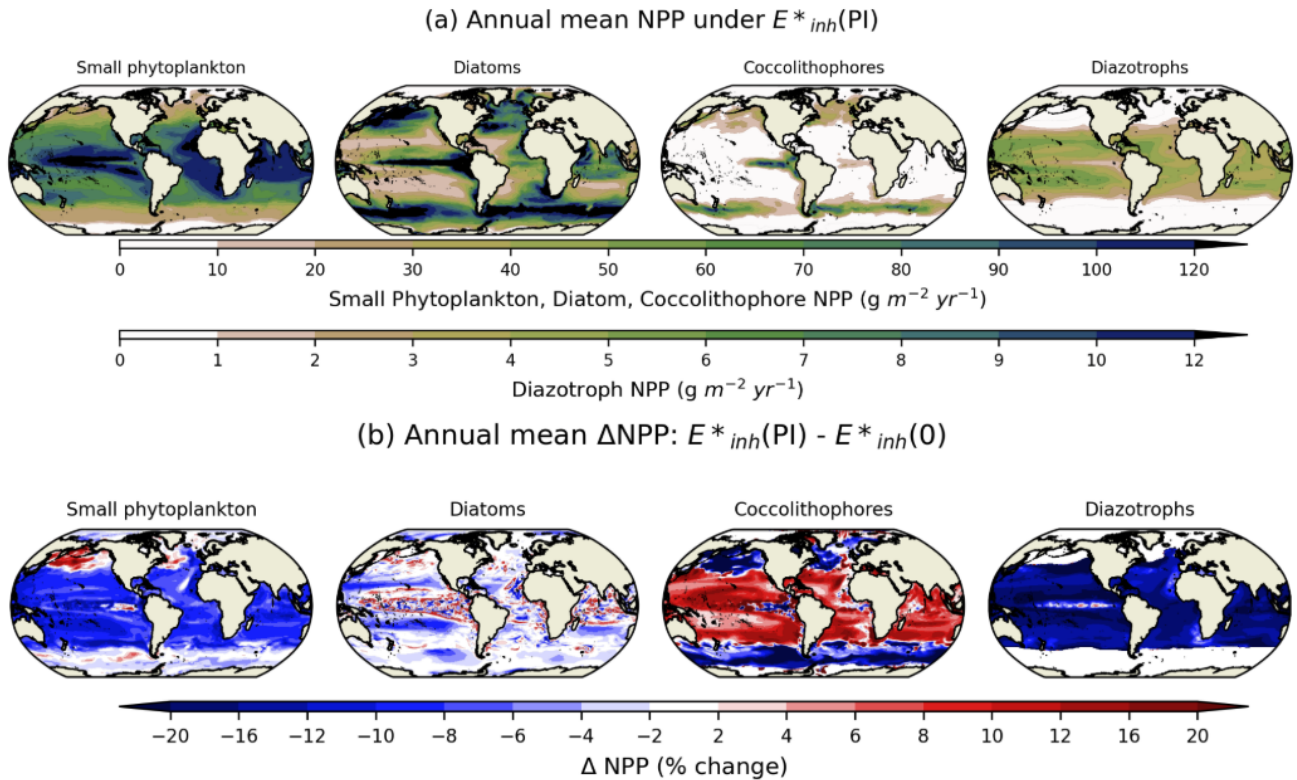


Figure 4. (a) The spatial distribution of 5 year annual mean productivity vertically integrated over the top 150 m ($\text{g C m}^{-2} \text{ yr}^{-1}$) in the $E^*_{inh}(\text{PI})$ simulation for small phytoplankton, diatoms, coccolithophores, and diazotrophs. (b) Percent change in annual mean NPP for $E^*_{inh}(\text{PI}) - E^*_{inh}(0)$ and (c) $E^*_{inh}(20\times \text{PI}) - E^*_{inh}(\text{PI})$ for small phytoplankton, diatoms, coccolithophores, and diazotrophs.

(Figure 4c). Under elevated UV radiation ($E^*_{inh}(20\times \text{PI})$), diatom NPP declines slightly relative to preindustrial NPP in some areas, but increases in many parts of the equatorial Pacific. Here, Coccolithophores are far more productive in the subtropics and tropics where small phytoplankton experience a large magnitude decrease in NPP with increasing UV radiation (Figure 4e), relieving nutrient limitation and allowing for the growth of diatoms. At 20x PI UV levels, coccolithophores show large declines in NPP relative to the preindustrial UV case in the subpolar Southern Ocean, North Pacific, and North Atlantic, up to a 15% decline in productivity compared to the simulation with $E^*_{inh}(0)$ forcing.

While UV inhibition in the top $\sim 15\text{--}35$ m of the ocean drives most of the a global decline of phytoplankton NPP with increasing UV radiation, whereas phytoplankton NPP an increase in productivity below this depth tends to increase compensates for the near-surface decline in many regions. Figure 5 shows the UV-radiation driven change in global NPP at each depth level and month over the course of 5 years (under $E^*_{inh}(20\times \text{PI}) - \text{PI}$ compared to $E^*_{inh}(\text{PI})$; expressed as percent change 0), expressed as a percent change. The top layer of the ocean (mid-point of 5 m depth) experiences a 35 up to a 15% reduction

440 in NPP, compared to only a ~~1-22-4%~~ decrease in NPP in the model's ~~2nd-4th~~ layer (mid-point of ~~15 m~~), and a ~~6.535 m~~ (Figure 5). Deeper levels of the ocean experience a surge in productivity in response to increasing UV radiation (e.g., an 8% increase in NPP in the model's ~~3rd~~ layer (mid-point of 25m)(Figure 5) at 95 m). UV-driven decreases in phytoplankton biomass (not shown; similar to NPP) in the top ~~two~~ layers allow for an increase in PAR at deeper layers due to a reduction in phytoplankton shading. UV-driven decreases in nutrient uptake in the surface layers (not shown) relieves nutrient limitation
445 throughout the mixed layer.

At high latitudes, NPP below the surface can be enhanced by more than 20% under elevated UV radiation (Figure 5b). While high albedo sea ice offers protection from UV radiation in CESM2-UVphyto, phytoplankton productivity underneath thin sea ice in the Southern Hemisphere is still reduced by more than 20% from August to October in E_{inh}^* (20x PI) compared to E_{inh}^* (PI). The reduction of near surface phytoplankton productivity promotes deeper blooms of Southern Ocean phytoplankton
450 productivity from December to March by allowing for PAR to penetrate deeper into the column, corresponding to more than a 10% increase in NPP below 35 m. This signal can be seen in the annual mean total phytoplankton change in NPP in Figure 5b. Subsurface increases in productivity partly compensate for near surface phytoplankton NPP decreases following UV radiation increases, but phytoplankton NPP declines near the surface dominate the upper ocean integrated net change in phytoplankton productivity in response to UV radiation. Coccolithophores' subsurface productivity enhancement is partly responsible for an
455 increase in their total column productivity across the subtropics and tropics.

Coccolithophores are ~~Certain types of coccolithophores can be~~ uniquely sensitive to UV radiation when CO₂ is elevated, which is represented in CESM2-UVphyto with ~~enhanced PIC/POC scaling~~. UV inhibition of coccolithophore growth rates ~~are~~ scaled by the inverse of PIC/POC^(1/6) (see Section 2.4). ~~Globally integrated coccolithophore NPP, while not a major driver of total phytoplankton NPP in our model (Figure 2b), is nevertheless influenced by UV radiation. In the E_{inh}^* (PI) simulation, global coccolithophore NPP is 3.5 Pg C yr⁻¹, decreasing to 2.9 Pg C yr⁻¹ in the E_{inh}^* (20x PI) simulation, a ~17% decline (Figures 2b,7). As atmospheric CO₂ increases, UV radiation engenders larger decreases in global coccolithophore NPP: a ~20% decrease at 400 ppm, a ~24% decrease at 600 ppm, and a ~25% decrease at 900 ppm in the E_{inh}^* (20x PI) simulation relative to the E_{inh}^* (PI) simulation (Figure 7). As atmospheric CO₂ and thus the aqueous CO₂ concentration increases, the PIC/POC distribution in the modeled ocean changes of simulated coccolithophores shifts (Figure 6), exposing a~~
465 ~~greater proportion of coccolithophores to UV radiation. PIC/POC shows a bimodal distribution, with peak densities at near 0 and 1.0 (Figure 6). With increasing CO₂, a greater proportion of thin-shelled coccolithophores are characterized as "naked" (PIC/POC<0.05), while the thick-shelled coccolithophores (PIC/POC≈1.0) see a shift in their distribution to lower PIC/POC values, akin to shell thinning (Krumhardt et al., 2019). This shell thinning makes the coccolithophores more susceptible to UV radiation, and thus coccolithophores experience larger UV-driven productivity declines when CO₂ is elevated-~~

470 Globally integrated coccolithophore NPP, while not a major driver of total phytoplankton NPP in the model (Figure 7).

In a simulation without PIC/POC scaling forced by E_{inh}^* (PI) (2b), is nevertheless influenced by UV radiation and CO₂ concentration. Under atmospheric CO₂ concentrations of 284 ppm, globally integrated total phytoplankton NPP is 55.6 global coccolithophore NPP is 4.5 Pg C yr⁻¹, less than a 1% change from the simulation with PIC/POC scaling. Despite little change in the sum of all phytoplankton, Under E_{inh}^* (PI) and atmospheric CO₂ of 284 ppm, global coccolithophore NPP

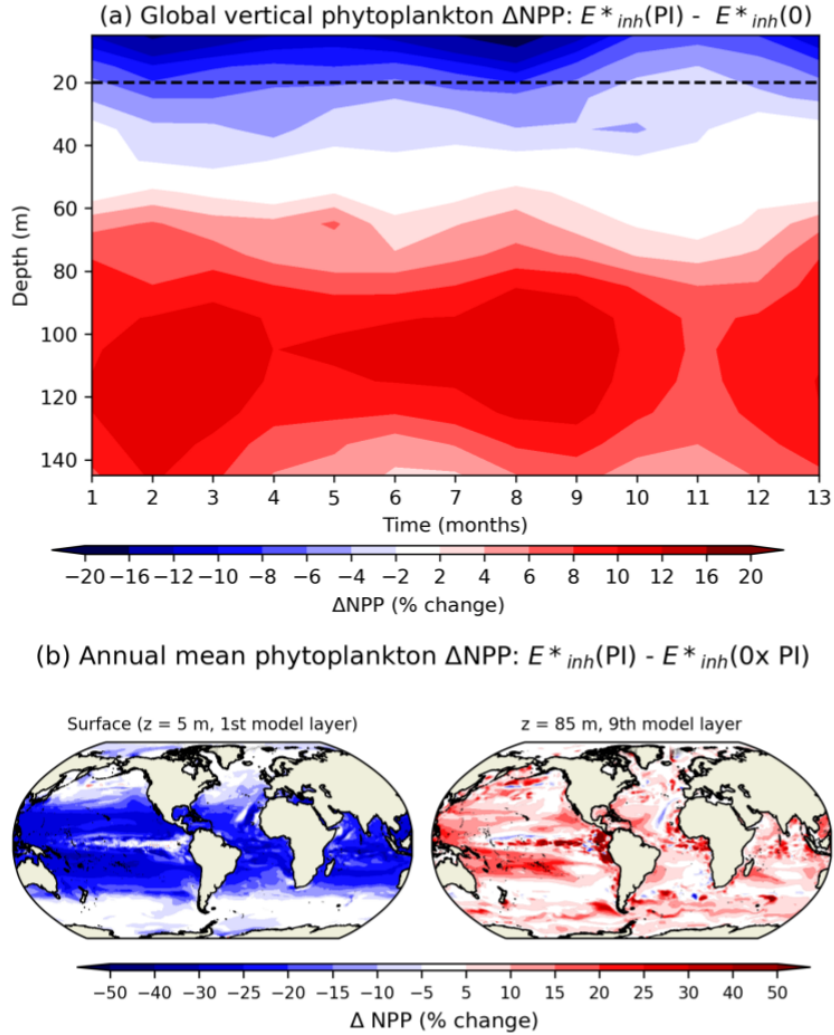


Figure 5. (a) UV-driven change in global-mean NPP ($\text{g C yr}^{-1} \text{m}^{-1}$) as a function of depth, calculated as the NPP from the $E^*_{inh}(20\times \text{PI})$ simulation minus the NPP from the $E^*_{inh}(0\times \text{PI})$ simulation over 5 years of simulation. The dashed black line represents the average depth where E^*_{inh} -UV-B radiation attenuates to 1% of its value-at-the-surface value. (b) Map of annual mean NPP percent change from the $E^*_{inh}(20\times \text{PI})$ simulation minus the NPP from the $E^*_{inh}(0\times \text{PI})$ simulation at (left) 5 m and (right) 35-85 m depth over 5 years of simulation.

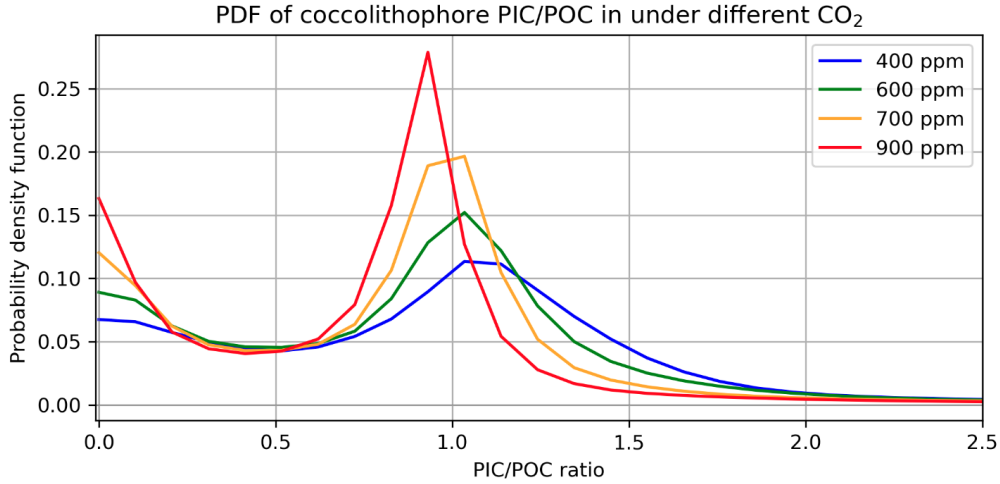


Figure 6. The probability density function for annual mean PIC/POC, weighted by coccolithophore biomass, for a 10-year spin-up where CO_2 is 400 ppm, 600 ppm, 700 ppm, and 900 ppm.

declines by approximately 8% (3.8 to 3.5) increases by 3.6% to 4.6 Pg C yr^{-1} , see (Figure 2b, Figure 7) from $E_{inh}^*(0)$ to $E_{inh}^*(\text{PI})$ with PIC/POC scaling, compared to 0.3% without. Small phytoplankton and diatoms experience increases in NPP when coccolithophore growth rates are scaled by the inverse of $\text{PIC/POC}^{(1/6)}$ even under pre-industrial UV radiation (not shown). In the PIC/POC scaled $E_{inh}^*(20\times \text{PI})$ simulation, globally integrated total phytoplankton NPP declines to 51.2 Pg C yr^{-1} , less than a 0.5% change from a $E_{inh}^*(20\times \text{PI})$ simulation not scaled by coccolithophore PIC/POC. Coccolithophore productivity declines by 25% with PIC/POC scaling in the simulation with $E_{inh}^*(20\times \text{PI})$ forcing compared to one with $E_{inh}^*(\text{PI})$ simulation. Prior to the implementation of PIC/POC scaling, Under atmospheric CO_2 concentrations of 284 ppm, increasing UV radiation produces a 4% decline in globally integrated coccolithophore NPP in the surface ocean, but an overall increase in upper-ocean integrated global coccolithophore NPP declined by only 5% under $E_{inh}^*(20\times \text{PI})$ when compared to $E_{inh}^*(\text{PI})$. Coccolithophores exhibit relatively high (Figure 7), due to enhanced subsurface productivity. Coccolithophore NPP shows increasing sensitivity to UV radiation compared to other PFTs even under pre-industrial under higher atmospheric CO_2 concentrations using scaling derived from laboratory studies (Xu et al., 2016).

Small phytoplankton, diatoms, and diazotrophs all benefit in response to diminished coccolithophore growth, and global integrated total phytoplankton NPP does not vary significantly as (Figure 7). Our two simulations with atmospheric CO_2 increases. Because coccolithophores with lower PIC/POC values are eliminated by high UV radiation under the scheme with PIC/POC scaling, a positive shift occurs in the globally averaged and biomass weighted coccolithophore PIC/POC over time under $E_{inh}^*(20\times \text{PI})$. After a year of $E_{inh}^*(20\times \text{PI})$ forcing, thin-shelled coccolithophores are seemingly eliminated, leaving behind thicker shelled coccolithophores in warmer locations. This shift leaves behind a smaller, but seemingly more resilient population of coccolithophores. concentrations of 700 ppm and 900 pm generate 11% and 13% lower global surface

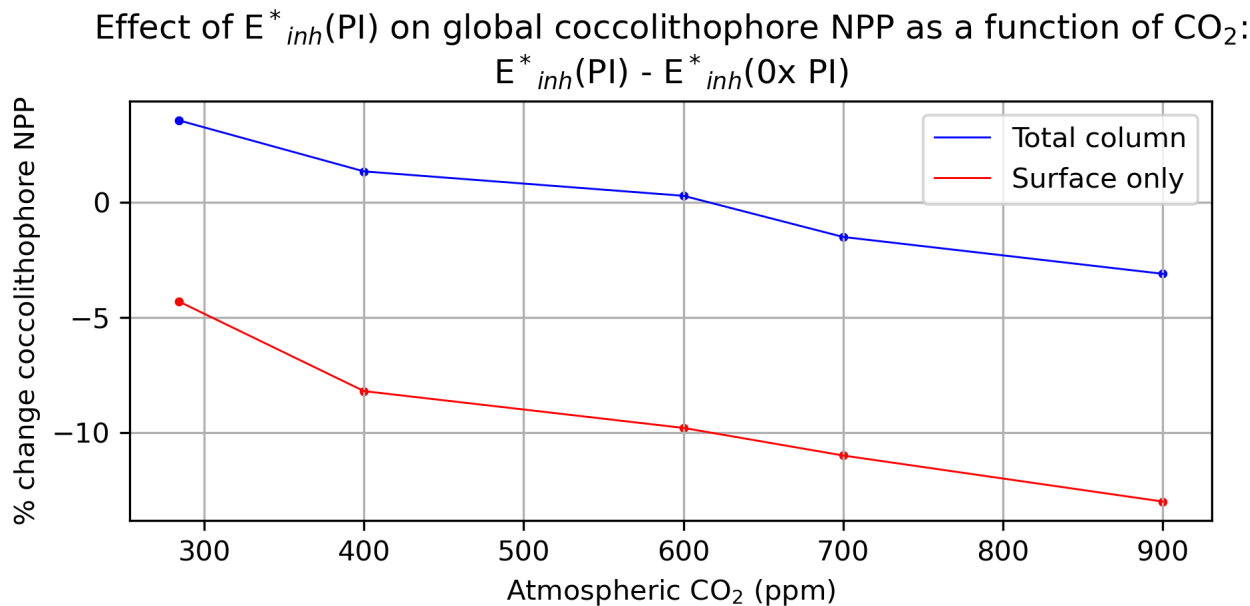


Figure 7. Annual mean coccolithophore net primary productivity percent change under simulation with $E^*_{inh}(20x PI)$ forcing compared to $E^*_{inh}(0x PI)$ with varying atmospheric CO_2 .

coccolithophore productivity, respectively, under pre-industrial levels of UV radiation compared to no UV radiation (Figure 7).

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The probability density function for annual mean PIC/POC, weighted by coccolithophore biomass, for a 10-year spin-up where CO_2 is 400 ppm, 600 ppm, 700 ppm, and 900 ppm. We further We assess the spatial heterogeneity in the phytoplankton NPP response to UV radiation under different atmospheric CO_2 concentrations using the core biomes defined by Fay et al. (2014). In general, coccolithophores tend to be most negatively impacted by UV radiation in the seasonally ice-covered and subpolar biomes of the north Pacific, north Atlantic, and Southern Ocean (Figure 8a). The abundance of coccolithophores in these biomes, coupled with their relatively low PIC/POC values mean that coccolithophores are especially responsive to UV radiation increases here. ~~Coccolithophores growing under elevated even under low levels of~~ atmospheric CO_2 concentrations (and thus have lower PIC/POC values), ~~experience higher levels of UV inhibition when UV is elevated and see even larger declines in NPP in the supolar north Pacific and Southern Ocean (Figure 8b). For example, in biome 16 (Southern Ocean Subpolar Seasonally Stratified), coccolithophore NPP declines by over 50% in December and January, which enhances diatom NPP in January and February. In contrast, coccolithophore NPP increases in response to UV radiation in subtropical and tropical biomes under low levels of atmospheric CO_2 , as small phytoplankton productivity declines (Figure 8e). In the tropical and subtropical biomes, in contrast, coccolithophore NPP increases with increasing atmospheric CO_2 . Under atmospheric CO_2 , even as UV radiation increases, driving decreases in small phytoplankton and diatom NPP of 900 ppm, most biomes~~ show a loss in coccolithophore productivity with increasing UV radiation (Figure 8b).

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Figure 8c shows monthly coccolithophore NPP for biome 16 across varying levels of E_{inh}^* . The coccolithophore bloom maximum occurs in February to March and is dampened by UV inhibition, especially under PIC/POC sealing, but there is no change in the timing of the bloom. No change in the timing of blooms is also true for all biomes that experience this bloom behavior, including biomes 1 (North Pacific Iee), 5 (West Pacific Equatorial), 7 (South Pacific Subtropical Permanently Stratified), 8 (North Atlantic Iee), 15 (illustrates the role of increasing CO₂ on coccolithophore NPP sensitivity to UV radiation in the Southern Ocean Subtropical Seasonally Stratified), and 16 (Southern Ocean Subpolar Seasonally Stratified). Several biomes exhibit a noticeable increase in productivity despite UV inhibition, including biomes 3 (North Pacific Subtropical Seasonally Stratified), 10 (North Atlantic Subtropical Seasonally Stratified), and 12 (Atlantic Equatorial). Prior to PIC/POC sealing, coccolithophores in biome 16 experienced a 14% decline in NPP under E_{inh}^* (20x PI) compared to E_{inh}^* (PI), which is in the accepted range of total NPP decline possible under the effect of the ozone hole, a smaller perturbation compared to the UV pulse in our experiments. Under PIC/POC sealing biome (SO-STSS; biome 15). Here, coccolithophore NPP declines by 60% in the same biome, demonstrating increased vulnerability in the coldest biomes.

As reductions under UV radiation are enhanced by 5-30% when atmospheric CO₂ is increased to 400 ppm, coccolithophores in biome 16 benefit from relieved carbon limitation more than they are impacted by thinner coccospheres. When CO₂ is increased increases from 284 ppm to 900 ppm, coccosphere thinning dominates and most high latitude regions experience a decline in coccolithophore productivity, while coccolithophores in subtropical and tropical biomes tend to benefit more from relieved carbon limitation with the largest enhancements in April, November and December (Figure 8b). Overall, the greatest percent change in coccolithophore NPP due to UV radiation occurs at high latitudes and parts of the equatorial Pacific, where cold temperatures and/or upwelling of carbon rich waters result in lower PIC/POC values, thinner coccospheres, and enhanced UV inhibition. In these same regions, small phytoplankton benefit and experience an increase in NPP, despite relatively high UV radiation. c).

4 Discussion

Changes in phytoplankton NPP are simulated in response to a pulse of UV radiation, with variations that occur as a function of latitude, depth, temperature, nutrient availability, and other phytoplankton characteristics. Globally integrated small phytoplankton NPP is particularly impacted by its large presence UV radiation due to high rates of productivity at low latitudes, where the simulated pulse of and high inhibition relative to the other biological weighting functions. Small phytoplankton benefit from UV radiation increases in the subpolar North Pacific, and spatial variability in the response to UV radiation is at its greatest. In evident across phytoplankton functional types. At pre-industrial levels of atmospheric CO₂, coccolithophore shell thinning is a non-factor except in some high latitude regions. In fact, because of coccolithophore resilience to UV radiation incorporated into the BWF used to compute UV inhibition, coccolithophores benefit at the expense of small phytoplankton across the entire mixed layer.

The simulations presented here use pre-industrial boundary conditions and therefore exhibit slightly less UV radiation compared to similar simulations with present day ozone distributions. The phytoplankton response in the surface ocean is

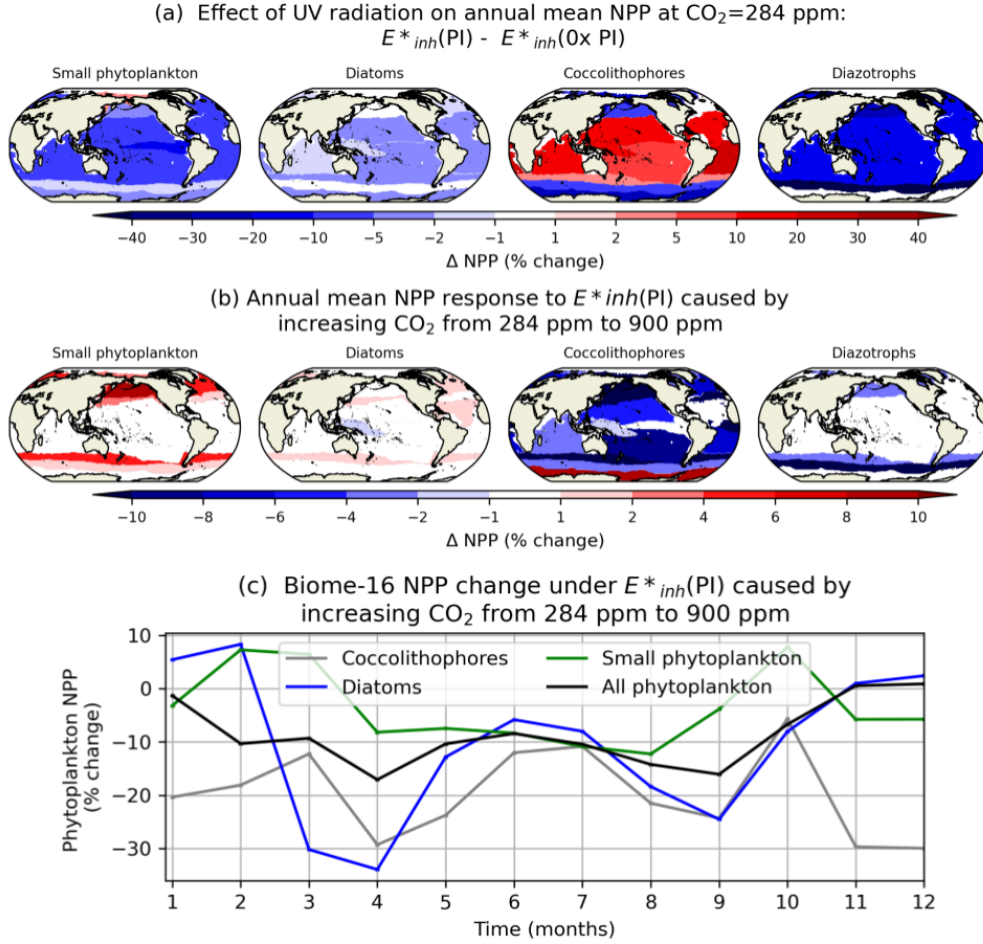


Figure 8. (a) Annual mean percent change in upper-ocean integrated NPP across 17 biomes under $E^*_{inh}(20\text{x-PI}) - E^*_{inh}(0\text{x PI})$ and with $\text{CO}_2=284$ ppm. (b) Annual difference in percent change in NPP across 17 biomes under $E^*_{inh}(20\text{x-PI}) - \text{CO}_2 - E^*_{inh}(900\text{-ppm}0\text{x PI}) -$ attributable to increasing CO_2 (from 284 ppm to 900 ppm). (c) Phytoplankton Different in monthly phytoplankton NPP annual-mean-percent change-for biome 16-15 (Southern Ocean IeeSubtropical Seasonally Stratified) under $E^*_{inh}(20\text{x-PI})$ for $\text{CO}_2=900\text{-ppm}$ compared- $E^*_{inh}(0\text{x PI})$ attributable to increasing CO_2 =from 284 ppm to 900 ppm.

likely to be enhanced in the present day compared to the ~~simulations examined here, small phytoplankton begin to be able to~~
545 ~~compete in pre-industrial, but would still be less than the E_{inh}^* (halogen) simulation.~~

Observational studies of regional phytoplankton productivity changes in response to ambient UV radiation range from
a 0.15% annual mean reduction in NPP south of the Polar Front in the Southern Ocean (Helbling et al., 1992) to a 4% to
7% reduction in NPP during austral spring across the Southern Ocean (Prézelin et al., 1994). Smith et al. (1992) found a 3%
reduction in a population of *Phaeocystis* when exposed to typical UV radiation levels, equivalent to an ozone layer with a
550 thickness of 350 dobson units (DU), which is higher than typical values simulated under E_{inh}^* (PI) (310 DU). In the E_{inh}^* (PI)
simulation, some parts of the Southern Ocean experience up to a 15% decline in NPP, adjacent to areas with an equally large
increase in productivity. On average the Southern Ocean ~~where the decline of coccolithophores has relieved nutrient limitation~~
~~in spite of temperature limitation. In an Antarctic ozone hole scenario where UV radiation is enhanced in experiences a 5%~~
~~to 10% decline in annual mean productivity, driven by coccolithophore decline. Small phytoplankton, the PFT most closely~~
555 ~~resembling *Phaeocystis*, experience a 3% decline at most and benefit in areas with the greatest coccolithophore loss. This is~~
~~on the lower end of the Smith et al. (1992)'s findings for *Phaeocystis* but precise validation is made difficult by the Southern~~
~~Ocean, diatoms and coccolithophores may be more impacted. We do not conduct these simulations here but provide a tool for~~
~~such experiments in the future.~~

~~Few examples of extreme UV pulses have occurred during the existence of modern observation systems for validation~~
560 ~~purposes, but our UV pulse simulation results generally fall within the large uncertainty range of existing laboratory and~~
~~observational studies of phytoplankton under ambient UV radiation (Helbling et al., 1992; Smith et al., 1992), as well as the~~
~~Southern Hemisphere ozone hole (Prézelin et al., 1994). In simulations with extreme levels of UV radiation at high latitudes,~~
~~coccolithophore productivity responses to UV radiation are on the high end of existing observational studies which typically~~
~~involved lower amounts of UV radiation. The primary difficulty lies in the lack of information regarding how phytoplankton~~
565 ~~across most of the world, which did not experience an ozone hole, would be impacted by increased UV radiation.~~

The development of CESM2-UVphyto is challenged by our understanding of how phytoplankton respond to increased UV
radiation. The calculation of UV damage (E_{inh}^*) in CESM2-UVphyto is specific to each phytoplankton type, yet only a small
number of laboratory studies report BWFs for the modeled PFTs. ~~No BWF was~~ ~~We caution that the model is somewhat~~
~~sensitive to the exact BWF employed; the PFTs in MARBL represent many different types of phytoplankton while the BWFs~~
570 ~~are based on laboratory experiments with a single species. Furthermore, there is a limited temperature range over which~~
~~BWFs are reported, typically between 20°C and 26°C, which can affect the modeled representation of UV inhibition at cold~~
~~temperatures. No BWFs are available for diazotrophs and only one BWF could be found for coccolithophores. there exist~~
~~different BWFs for coccolithophores in the literature. BWFs are typically determined from short-term growth inhibition, which~~
~~may not reflect the effects of direct damage to DNA over longer timescales. Over longer simulations under pre-industrial UV~~
575 ~~radiation, inaccuracy in the BWFs may lead to drifts in nitrogen, alkalinity, calcium carbonate, etc. compared to the observed~~
~~ocean. However, pre-industrial levels of UV radiation are unlikely to cause significant drifts due to the relatively low impacts~~
~~to phytoplankton productivity. Further research developing BWFs with laboratory studies that are more tailored to the species~~
~~used to represent each PFT in MARBL and across larger temperature ranges would narrow uncertainties in simulating UV~~

inhibition of photosynthesis. [CESM2-UVphyto can be used to quickly assess how new laboratory-derived BWFs for different phytoplankton species would affect phytoplankton biomass, carbon export, marine organisms at upper trophic levels that are supported by phytoplankton.](#)

CESM2-UVphyto horizontal and vertical resolution may also play a role in the fidelity of our simulations. At 1 degree nominal horizontal resolution, mesoscale features and some coastal processes are not represented, an absence that potentially impacts the timing and spatial scale of phytoplankton blooms. Scaling UV radiation penetration into the ocean based on wave properties was not possible in CESM2-UVphyto, but higher resolution modeling with parameterizations accounting for the scattering of UV when encountering waves and whitecaps could improve the simulation of UV radiation penetration into the ocean. We expect regions with significant wave activity to likely experience an overestimate in UV inhibition, while calmer, subtropical waters likely experience an underestimate in our model simulations. Finally, because UV attenuates so quickly with depth, the available 10 m vertical spacing in CESM2-UVphyto may produce small inaccuracies in UV inhibition of photosynthesis that can affect the vertical profile of phytoplankton and as a result, the shading of PAR and PAR amounts deeper in the water column. [Implementation of UV inhibition in a model with higher vertical resolution would likely resolve these processes with greater accuracy.](#) Zooplankton biomass is not considered in shading equations for PAR or UV radiation, potentially leading to small errors in radiation propagation. The absence of chlorophyll in zooplankton minimize its effectiveness at intercepting PAR, but its effects on UV radiation is less clear.

5 Conclusions

We have implemented inhibition of photosynthesis from UV radiation for four different types of phytoplankton in the versatile ocean biogeochemistry model MARBL, which can be incorporated into a number of global climate models. The implementation requires the computation of photosynthetic UV damage using biological weighting functions integrated over the wavelengths of UV radiation within the atmospheric model. We explored ~~a large parameter space of~~ global E_{inh}^* values ~~to ranging~~ [from a healthy, pre-industrial stratosphere to a very depleted stratosphere to](#) understand the performance of our modifications at extremes.

CESM2-UVphyto is the first fully coupled Earth system model to calculate and consider UV inhibition of photosynthesis among phytoplankton. Increased UV radiation from the ozone hole likely impacted Southern Ocean phytoplankton, but only simple models have been used to quantify this response. UV radiation may have shaped the recovery of ecosystems during the extinction event at the K-Pg boundary, but simulations of this event have not typically included the role of increased UV radiation after an asteroid impact. CESM2-UVphyto is capable of simulating the emissions from an asteroid impact and the hypothesized pulse of UV radiation afterwards. Simulating the impact of a pulse of UV radiation and its role towards an extinction event in an Earth system model is one example of a use case that can help inform interpretations of proxy records of marine organisms in the years afterwards. Furthermore, quantifying mechanisms of past extinction provides context for ongoing anthropogenic climate change which may involve enhanced UV inhibition in increasingly stratified ocean layers. Other stratospheric aerosol injection events such as volcanic eruptions, large-scale wildfires, geoengineering, or even nuclear

war may pose further risks to the stratospheric ozone layer. CESM2-UVphyto provides a modeling tool for quantifying ocean ecosystem impacts of these events.

Code and data availability.

615 The code modifications to the CESM [and Jupyter notebook entitled manuscript_figures.ipynb to generate all figures](https://github.com/coupewx/CESM2-UV/tree/coupewx-cesm2-uvphyto-01) are stored on [GitHub at https://github.com/coupewx/CESM2-UV/tree/coupewx-cesm2-uvphyto-01](https://github.com/coupewx/CESM2-UV/tree/coupewx-cesm2-uvphyto-01) [Zenodo at DOI: 10.5281/zenodo.14025743](https://zenodo.org/record/14025743). The data used to produce figures in the main text and supplemental is archived on Zenodo ([at DOI: 10.5281/zenodo.11127431](https://zenodo.org/record/11127431)); ~~A Jupyter notebook to generate all figures can be found at https://github.com/coupewx/CESM2-UV/blob/master/notebooks/manuscript_fig~~

Author contributions.

620 NL conceptualized the study. CB added TUV to the atmospheric model. LG, JC, and NL determined biological weighting functions for use in MARBL. JC implemented biological weighting functions into TUV. JC designed and implemented UV inhibition in MARBL with assistance from ML. KK provided experimental 4p2z version of MARBL. JC ran the model simulations. JC analyzed simulation results and prepared the manuscript. JC, et al., assisted in preparing and reviewing the manuscript.

625 *Competing interests.*

We declare no competing interests.

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