

Effect of plankton composition shifts in the North Atlantic on atmospheric pCO₂

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Key Points:

- Biological production decreases significantly in the high latitude North Atlantic in CESM2 under the SSP5-8.5 scenario.
- Plankton type dominance shifts from diatoms to small phytoplankton.
- A positive feedback loop is diagnosed where changes in the physical system decrease biological production, reducing oceanic uptake of CO₂.

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Abstract

Marine carbon cycle processes are important for taking up atmospheric CO₂ thereby reducing climate change. Biological production is an important pathway of carbon from the surface to the deep ocean where it is stored for thousands of years. Climate change can interact with marine ecosystems via changes in the ocean stratification and ocean circulation. In this study we use the Community Earth System Model version 2 (CESM2) results to assess the effect of a changing climate on biological production and plankton composition in the high latitude North Atlantic Ocean. We find a shift in plankton type dominance from diatoms to small phytoplankton which reduces net primary and export productivity. Using a conceptual carbon-cycle model forced with the CESM2 results, we give a rough estimate of a positive plankton composition-atmospheric CO₂ feedback of approximately 60 GtCO₂/K warming in the North Atlantic which affects the 1.5 K and 2.0 K warming safe carbon budgets.

Plain Language Summary

The marine carbon cycle is important for taking up carbon from the atmosphere and thereby lowering atmospheric CO₂ concentrations. One of the ways the marine carbon cycle transports carbon from the surface to the deep ocean is biological production. Once in the deep ocean, carbon can be stored for thousands of years. Biological production is dependent on environmental conditions such as nutrient availability and ocean temperature, which can be affected by increasing atmospheric CO₂ concentrations. This can lead to a positive (negative) feedback loop, where increasing CO₂ concentration decrease (increase) biological production which in turn decreases (increases) uptake of CO₂ by the ocean, effectively increasing (decreasing) atmospheric CO₂ concentrations. Here, we find in an Earth System Model that under a high emission scenario, biological production decreases significantly in the high latitude North Atlantic Ocean which is primarily the result of a shift in dominant phytoplankton type in this region. Larger diatoms, which are relatively efficient in exporting carbon, are replaced by small phytoplankton which are less efficient. By using a conceptual carbon cycle model, we identify a positive feedback loop where the decrease in biological production increases atmospheric CO₂ by approximately 60 GtCO₂ per degree warming.

1 Introduction

To avoid tipping behavior in the Earth system, it is important to keep warming of our planet to a maximum of 1.5 to 2°C (Lenton et al., 2019). Policymakers need to know how much carbon we can still emit before we exceed this warming. However, estimates of this safe carbon budget are difficult and subject to large uncertainties because the Earth system has many processes and feedbacks that are not completely understood yet (Matthews et al., 2021).

The marine carbon pumps (physical, biological and carbonate) are currently responsible for taking up 25-40 percent of anthropogenic carbon (Sabine et al., 2004; DeVries et al., 2017). It is estimated that biological production in the ocean exports approximately 11 GtC yr⁻¹ to the deep ocean (Sanders et al., 2014) and that without this export, atmospheric pCO₂ values would be 200-400 ppm higher (Ito & Follows, 2005; Henson et al., 2022). This export production (EP) is dependent on the net primary productivity (NPP). It also depends on plankton composition, since different plankton species have different remineralization depths (Morán et al., 2010; Li et al., 2009; Marinov et al., 2013).

Both EP and NPP are strongly dependent on temperature, ocean circulation, stratification and nutrient input (Doney et al., 2011) which can all affect plankton composition. This is important because changes in plankton composition can transfer through

the food web affecting fish and mammals (Richardson & Schoeman, 2004; Beaugrand, 2009) which can affect fishery yields. Furthermore, plankton composition also affects EP which indirectly influences the air-sea gas exchange of CO_2 that could result in a positive feedback loop under climate change (Cabr   et al., 2015). In such a feedback higher CO_2 levels change plankton composition, reducing EP and thus the uptake of CO_2 by the ocean. Finally, a changing plankton composition is one of the hypotheses suggested to explain (part of) the atmospheric pCO_2 (80-100 ppm) variations in the Pleistocene glacial-interglacial cycles (Archer & Maier-Reimer, 1994; Kohfeld et al., 2005), showing the potential of this feedback to affect the climate.

Though climate change is likely to affect plankton stocks, the extent is still uncertain (Osman et al., 2019). Expected effects of global warming are changes in NPP (Behrenfeld et al., 2006), reduced nutrient concentrations in the surface ocean due to stronger stratification (Bopp et al., 2001, 2005; Fu et al., 2016), and plankton composition changes, the latter also due to changing co-limitation of light and nutrients (Marinov et al., 2013; C. M. Moore et al., 2013). Furthermore, on longer timescales, severe nutrient trapping in the Southern Ocean is possible, which reduces biological production over most of the ocean (J. K. Moore et al., 2018). However, uncertainties remain in most (model) studies. This is because the complex timing of blooms are difficult to simulate in highly seasonal regions such as the high latitudes (Martinez et al., 2011), and also because ecosystem models that have more extensive plankton dynamics show larger community composition shifts with climate change (Dutkiewicz et al., 2013; Fu et al., 2016). Comparing CMIP6 models with CMIP5 models, we see an increase in intermodel spread in both NPP and EP (Kwiatkowski et al., 2020; Tagliabue et al., 2021; Henson et al., 2022), highlighting the complexity of the system.

One of the regions that is projected to be affected significantly by climate change is the North Atlantic, a region where biological processes are known to be important for gas exchange of CO_2 (Bennington et al., 2009). Observational studies suggest that plankton composition shifts are already occurring in this region (Hilligs   et al., 2011; Rivero-Calle et al., 2015). Model simulations under high emission scenarios project that the future North Atlantic will have relatively low warming rates, relatively high acidification rates and a (medium to large) decrease of subsurface oxygen (Bopp et al., 2013). In addition, the stratification and ocean circulation are projected to change, such as a decrease in the strength of the Atlantic Meridional Overturning Circulation (AMOC), which could possibly result in a collapse of plankton stocks in the North Atlantic (Schmittner, 2005). These projected changes would lead to large decreases of NPP and EP (Steinacher et al., 2010; Bopp et al., 2013).

The main novel aspect of this study is to provide an estimate of the plankton composition-atmospheric pCO_2 feedback (Cabr   et al., 2015) using climate model simulations for a high emission scenario (SSP5-8.5). We aim to answer the following questions: How does biological production respond to higher pCO_2 levels? Does this lead to a positive or a negative feedback on atmospheric CO_2 ? And lastly, what does this imply for the safe carbon budget? To investigate these issues we have used two models, the Community Earth System Model v2 (CESM2) and the Simple Carbon Project Model v1.0 (SCP-M) as described in Section 2. Results are shown in Section 3 and are summarized and discussed in Section 4.

2 Method

We analyse output from the Community Earth System Model v2 (CESM2, Danabasoglu et al. (2020)) simulations as used in the Coupled Model Intercomparison Project 6 (CMIP6, Eyring et al. (2016)). This model includes the CAM6 atmospheric model, the CLM land model, the CICE sea-ice model, the POP2 ocean circulation model, and the MARBL ocean biogeochemistry model. Both POP2 (Smith et al., 2010) and MARBL (Long et al., 2021)

are run on a displaced Greenland pole grid at a nominal 1° horizontal resolution, with 60 non-equidistant vertical levels. In MARBL, several elemental cycles, three explicit phytoplankton functional groups (small phytoplankton, diatoms, and diazotrophs), one implicit phytoplankton group (calcifiers), and one zooplankton group are simulated. We analyse output of a single member CESM2 simulation (Danabasoglu, 2019) which is driven by greenhouse gas emissions according to the SSP5-8.5 scenario (B. C. O'Neill et al., 2020; Green et al., 2021). Since it is an emission driven case, atmospheric $p\text{CO}_2$ is affected by feedbacks from the land and ocean reservoirs of carbon. The simulation period is from 2015-2101 and analysis results in section 3 are based on monthly and yearly mean data.

Generally, CESM2 is one of the better performing Earth System Models when ocean biogeochemistry is considered globally (S  f  rian et al., 2020). MARBL, however, has some biases due to deficiencies in the ocean circulation model (POP2). In particular, the too sluggish deep ocean circulation in POP2 causes nutrient trapping in the deep North Pacific Ocean. In MARBL, this results in low abundances of oxygen throughout the deep Pacific Ocean, which causes organic matter to be remineralized via nitrogen, negatively affecting the quality of the nitrogen cycle simulation. This large bias was fixed by adjusting the stoichiometric ratios of organic matter in the Pacific Ocean so less oxygen is consumed by organic matter remineralization; with this fix, only local biases remain (Long et al., 2021).

The single CESM simulation is less suited to study the feedback processes between the marine carbon cycle and atmospheric CO_2 as, for example, the effects of the EP on outgassing cannot be easily isolated. To study these feedback processes in more detail, we use the Simple Carbon Project Model v1.0 (SCP-M) (C. M. O'Neill et al., 2019) as described in the Supplementary Information including adaptations from (Boot et al., 2022). The SCP-M consists of seven ocean boxes, one atmosphere box and two terrestrial reservoirs of carbon (Fig. S1) in which many carbon cycle processes are captured in a parameterized way. Processes in the model that affect dissolved inorganic carbon (DIC) and alkalinity (Alk) are the ocean circulation, biological production, calcium carbonate production and dissolution, river fluxes, sediment fluxes and the air-sea gas exchange of CO_2 (DIC only).

3 Results

The prescribed emissions (in Pg CO_2 per year) top in the year 2085 and decrease afterwards (Fig. S2a). By the year 2100, 88 GtC has been emitted into the atmosphere (Meinshausen et al., 2020). Under the influence of the emissions and the exchange with the land and the ocean, the atmospheric CO_2 concentration in the CESM simulation increases from 400 ppm in 2015 to 1069 ppm in 2100 (Fig. S2b). Part of this carbon (Fig. S3a) is taken up by the terrestrial biosphere (6 %), and part by the ocean (6 %). Over time, relatively less carbon is taken up by these two reservoirs, which means more remains in the atmosphere (Fig. S3b).

The changes in the global air-sea gas CO_2 exchange are shown in the upper panels of Fig. 1, where a positive sign indicates CO_2 transfer into the ocean. Whereas almost the entire ocean takes up more (or gasses out less) carbon at the end of the century compared to present-day, the North Atlantic actually takes up less. This becomes even more clear when we compare globally integrated gas exchange with the gas exchange integrated over the North Atlantic. Air-sea gas exchange increases globally until the end of the century but in the North Atlantic, it starts to decrease around the year 2040 (Fig. S4), suggesting substantial carbon cycle changes in the North Atlantic.

The response in the North Atlantic stands out for several reasons. First of all, the warming rate of Sea Surface Temperature (SST) is relatively low in the North Atlantic, and SSTs even decrease locally (Fig. S5). There are also large changes in the annual max-

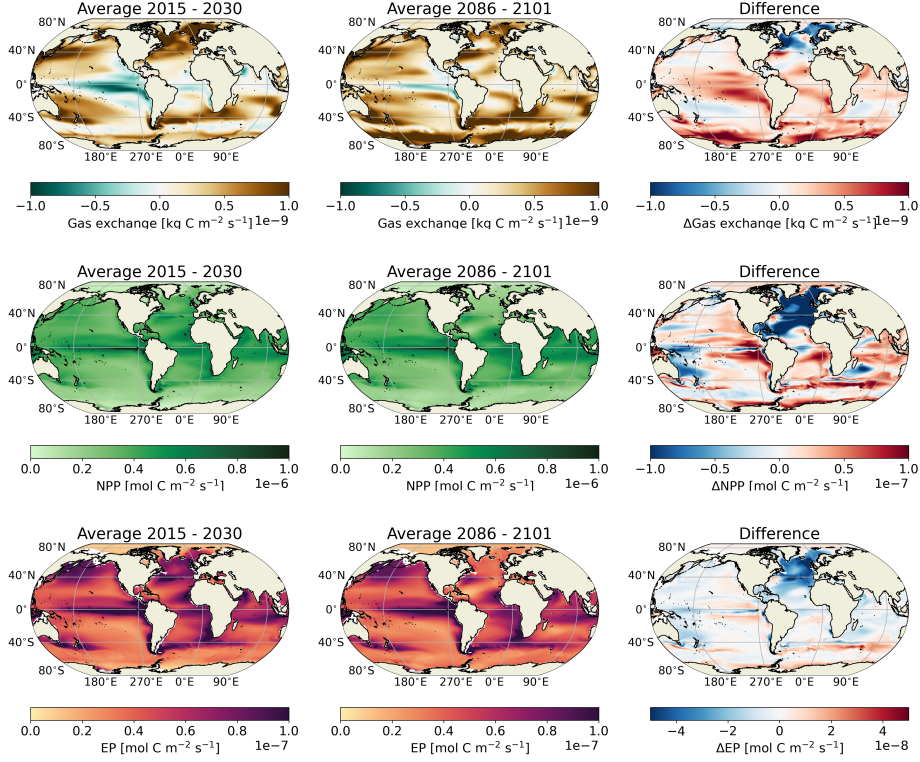


Figure 1. Changes in carbon-cycle relevant quantities in the CESM2 SSP5-8.5 emission driven simulation. Top row: gas exchange in $\text{kg C m}^{-2} \text{s}^{-1}$. Middle row: Net Primary Production integrated over top 100m in $\text{mol C m}^{-2} \text{s}^{-1}$. Bottom row: Export Production at 100m depth in $\text{mol C m}^{-2} \text{s}^{-1}$. Note the different scaling per row; within a row, each subplot is scaled in a similar way. Left column: averages over period 2015-2030; middle column: averaged over period 2086-2101; right column: differences between the two (middle - left).

imum mixed layer depth in the deep water formation regions around Greenland (Fig. S6). These are related to ocean circulation changes in particular a decrease in AMOC strength at 26.5°N from 17 Sv to 10 Sv over the simulation period (Fig. S7). We also see a stronger upper ocean stratification (Fig. S8), where stratification is measured here by the density difference between 200m depth and the surface.

There is a large decrease in both NPP and EP (at 100 m depth) in the North Atlantic and especially in the deep water formation areas around Greenland (Fig. 1). The decrease in EP cannot completely be explained by a decrease in NPP, since EP decreases more than NPP (Fig. S9). This suggests that the plankton functional types (PFTs) in MARBL respond differently in this region to climate change. Diazotrophs do not play a role here due to temperature limitation and hence we focus on changes in diatoms and small phytoplankton. We can determine the effect of these two PFTs by using the equation (used in CESM2) $NPP_i = \mu_{ref} T_f L_i V_i P_i$. Here i refers to the two PFTs (small phytoplankton and diatoms), μ_{ref} is the maximum C-specific growth rate (which is the same for both PFTs) and T_f is a temperature dependent function. Furthermore, L_i is a light limitation function, V_i a nutrient limitation function, and P_i is the biomass of PFT i . Both diatoms and small phytoplankton are limited by nitrogen (N), phosphorus (P), and iron (Fe); diatoms are also limited by silicate (Si).

In the beginning of the 21st century we see that diatoms are dominant in the high latitude North Atlantic (Fig. 2), whereas small phytoplankton are not very abundant. However, at the end of the century we see a change in PFT dominance as diatoms have almost completely disappeared, while the small phytoplankton NPP and biomass (Fig. S15) have increased. The large decrease in diatom NPP decreases total NPP in this region. This shift in plankton type dominance also explains why the EP decreases faster than the NPP (Fig. S9) since diatoms are more efficient in exporting carbon than small phytoplankton. Since diatoms become less abundant, the carbon transport from the surface to the deep ocean also becomes less efficient.

To investigate why the plankton composition changes in the North Atlantic, and why diatom NPP decreases, we look into what determines the production of the different PFTs. Both PFTs are generally nitrogen limited in this region, though nitrogen limitation is stronger for diatoms. Light limitation decreases by a small amount for the diatoms in the beginning of the 21st century before becoming more or less stable. Light limitation for small phytoplankton decreases throughout the entire century. The difference in light limitation explains mostly the co-limitation: diatom co-limitation of light and nutrients increases, whereas for small phytoplankton it decreases (Figs. S10-S11). We can also see this in the growth rate (NPP divided by biomass) of both PFTs (Fig. S12): the growth rate of diatoms peaks around 2035 and then gradually decreases, and the growth rate of small phytoplankton keeps on increasing.

The reduced growth rate of diatoms does not completely explain the decrease in NPP and biomass, since the biomass of diatoms decreases throughout the entire period (Fig. S13f), while the growth rate of diatoms first increases (Fig. S12). Another reason for the decrease in biomass is advective transport of diatoms out of the North Atlantic (Fig. S13). Looking at the advective fluxes of diatom biomass over the region (45°-70°N × 270°-0°E), we can see that in the beginning of the 21st century relatively much biomass is lost due to advection over the southern and eastern boundaries of this region which explains the decreasing NPP over this time period. Total advection decreases mostly due to reduced biomass concentrations near the southern boundary (Fig. S13d, e). Small phytoplankton biomass is not affected by this advection, because biomass concentrations are low in the beginning of the boundary of this region century and only increase at the southern boundary of the region when diatom biomass decreases (Fig. S14). Eventually, due to the reduced growth rate, the biomass of diatoms does not recover. This causes the decrease in diatom NPP and explains why small phytoplankton are able to outcompete diatoms in this region utilizing the nutrients not used by diatoms anymore.

The changes in NPP and EP affect the concentrations of DIC and Alk. These two tracers affect the pCO₂ of the surface ocean, and thus the gas exchange with the atmosphere. Within CESM, it is difficult (without further simulations) to determine the effect of the reduced NPP and EP on the air-sea gas exchange and atmospheric pCO₂ as the latter quantity is determined by many other processes which cannot be separated. This effect, however, is crucial for establishing the sign of the plankton composition atmospheric CO₂ feedback associated with changes in EP. To assess the feedback strength, we use the SCP-M model in combination with the CESM2 data.

Compared to the original model (C. M. O'Neill et al., 2019), we updated the SCP-M forcing files for the period 2015-2101 to represent the SSP5-8.5 scenario. We initialize the SCP-M with DIC, Alk and atmospheric CO₂ data from the CESM2 simulation of the year 2015. For the other tracers and the terrestrial biosphere initial conditions are taken from a run performed up until 2014 with historical emissions. The SCP-M captures less dynamics than the CESM2 due to reduced model complexity. We therefore first determine how large this term is to be able to separate this from the feedback strength (Fig. 3e,f). The relative uncaptured processes by the SCP-M amounts up to approximately 8% of the total atmospheric CO₂ concentration of the CESM2. After determining the uncaptured dynamics, we determine the feedback strength by allowing both the DIC and

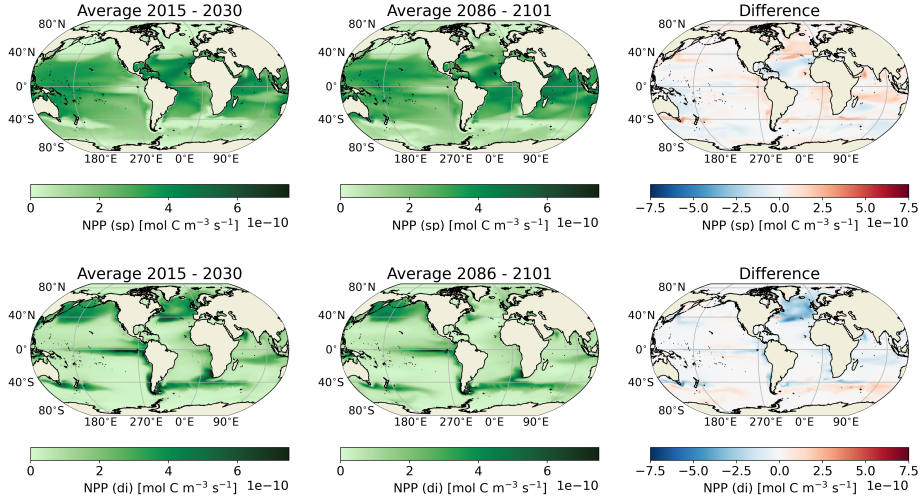


Figure 2. NPP averaged over top 100m in $\text{mol C m}^{-3} \text{s}^{-1}$ for small phytoplankton (top row) and diatoms (bottom row) for the period 2015-2030 (left), the period 2086-2101 (middle) and the difference between the two (right).

Alk biological fluxes to vary as a function of atmospheric pCO_2 following a fit to CESM2 output (Fig. 3c,d). This fit represents the rate of change of DIC and Alk due to biological activity and the CESM2 output variables are averaged over the region $40^\circ\text{-}60^\circ\text{N} \times 270^\circ\text{-}30^\circ\text{E}$ in the top 150m of the water column (Fig. 3a,b).

Using our method we can give a first estimate of the order of magnitude of the feedback. We find that the effect of reduced NPP and EP causes variability in both DIC and Alk which results in a cumulative flux of approximately 294 GtCO_2 extra in the atmosphere in the year 2100, resulting in a 37.9 ppm higher CO_2 concentration in the atmosphere (Fig. 4). Over this time period global mean surface temperature rises 4.9 K (average 2096-2100 minus average 2015-2019). This process hence represents a positive feedback with a strength of $60 \left(\frac{294}{4.9} \right) \text{GtCO}_2/\text{K}$ warming where, due to increasing CO_2 concentrations, changes in the physical system such as an increase in stratification in the North Atlantic, result in an unfavorable environment for diatoms while small phytoplankton profit. This change in plankton composition decreases the flux of carbon from the surface to the deep ocean which increases DIC and decreases Alk concentrations in the surface ocean. The combined effect results in a decrease in the uptake of CO_2 in the ocean, further increasing atmospheric CO_2 concentrations.

4 Summary and discussion

In this study, we investigated the interaction of atmospheric pCO_2 and biological production in the Atlantic Ocean north of 45°N in an emission driven SSP5-8.5 scenario simulation in CESM2. We found that under these high emissions, net primary production (NPP) and export production (EP) decrease in this region. Similar results on NPP and EP have been obtained in CMIP5 simulations under the RCP8.5 scenario (Bopp et al., 2013). It was shown that in the CESM2 simulation, this could be attributed to reduced productivity of diatoms which could be explained by increasing co-limitation of light and nitrogen and decreasing biomass stocks. The increasing limitation was the result of stronger stratification in the North Atlantic, which could be partly explained by increasing atmospheric temperatures due to increasing atmospheric CO_2 levels. The shift

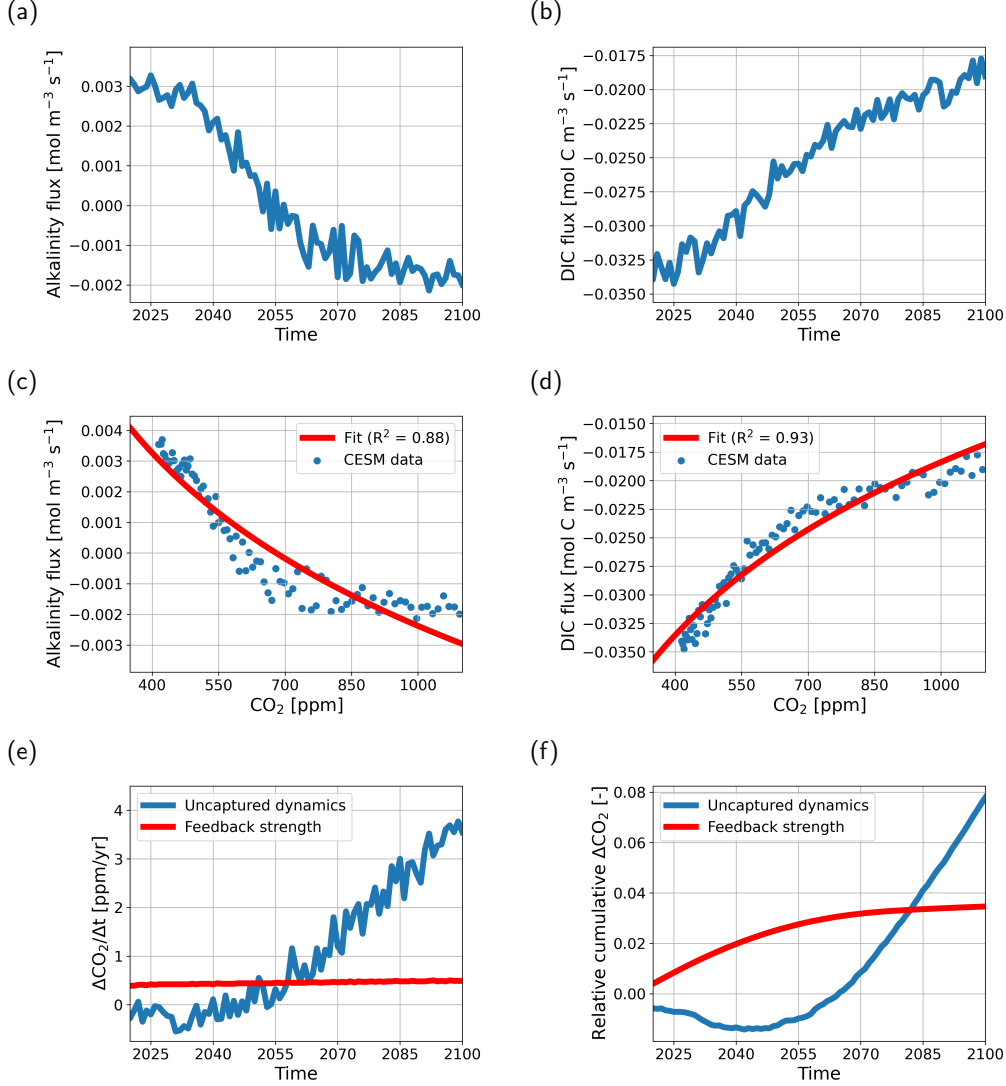


Figure 3. (a) Change of Alk flux in the region $40^{\circ}\text{--}60^{\circ}\text{N} \times 270^{\circ}\text{--}30^{\circ}\text{E}$ in the top 150m of the water column due to biological activity in the CESM2 versus time. (b) As in (a) but for DIC. (c) Blue markers represent CESM2 data as in (a) but versus atmospheric CO₂ concentration, and the red line represents a logarithmic fit to this data. (d) As (c) but for DIC. (e) The uncaptured dynamics for atmospheric CO₂ concentrations in ppm/yr in the SCP-M with respect to CESM2 in blue, and the feedback strength in red. (f) As in (e) but cumulative and relative to the atmospheric CO₂ concentration.

in plankton composition from larger diatoms to small phytoplankton is in agreement with theory and model results suggesting that small phytoplankton outcompete diatoms under increased nutrient stress (Marinov et al., 2013).

The results indicate the existence of a positive carbon cycle feedback where plankton composition plays a central role as shown in Fig. 4. Using an idealized carbon cycle model, we have made a first attempt to put an order of magnitude on the feedback

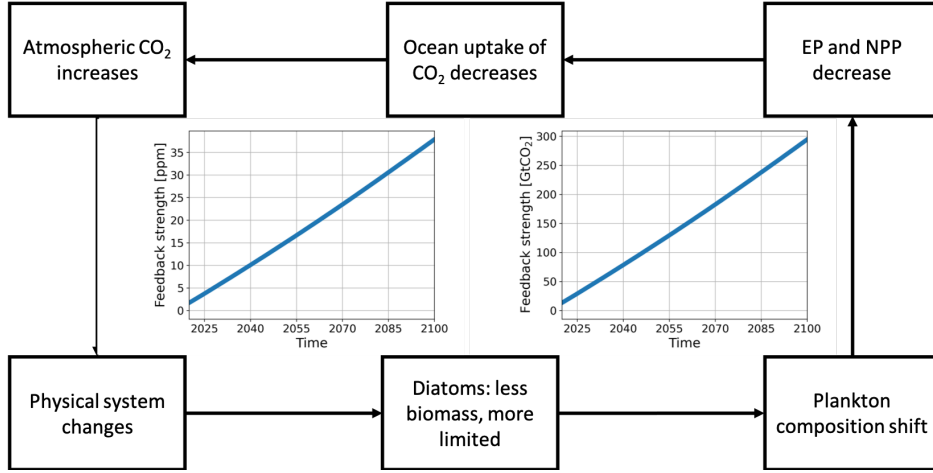


Figure 4. Positive feedback loop on how biological activity in the North Atlantic Ocean is coupled to atmospheric pCO₂. Left graph in the loop represents the increase of atmospheric pCO₂ due to the feedback loop in ppm. The right graph represents the equivalent cumulative change in air-sea gas exchange of CO₂ in GtCO₂.

strength. Obviously this method has several caveats since the SCP-M captures less dynamics than the CESM2 and it is therefore difficult to assess the reliability of the results. In our method, the uncaptured dynamics is quite sensitive to initial conditions and parameter values. However, the actual feedback strength is only sensitive to the original strength of the biological flux. Using this simple method, it was shown that this feedback results in an increase in atmospheric CO₂ of 37.9 ppm in 2100, which is equivalent to approximately 294 GtCO₂. To put this into perspective, this is slightly smaller than the increased CO₂ storage of ~ 336 GtCO₂ in the North Atlantic in the Last Glacial Maximum due to a more efficient biological carbon pump (Yu et al., 2019), meaning that the order of magnitude of our feedback strength is in a realistic range. This positive feedback (Cabr  et al., 2015) seems to be relatively small, but it needs to be taken into account when estimating the safe carbon budget in future climate change. The safe carbon budget is estimated to be 308 GtCO₂ for a peak global warming of 1.5 K, and 994 GtCO₂ for a warming of 2 K (van der Ploeg, 2018). Assuming the assessed feedback strength is correct, this feedback accounts for approximately 29% and 12% of the 1.5 K and 2.0 K warming safe carbon budget respectively. In summary, biological activity in the ocean is able to interact with the physical system and have an impact on variables such as global mean surface temperature via atmospheric CO₂ concentrations, with a substantial impact on our safe carbon budget. Furthermore, we want to stress that the numbers presented here should be viewed as an estimate on the order of magnitude of the feedback strength and not as an exact result because the used method to assess the feedback strength has multiple caveats.

Certainly this study has its limitations, as only a single Earth System Model with only a single member simulation for only one emission scenario is used. It might be very interesting to repeat such simulations and analysis with models having different plankton dynamics since responses of Earth System Models depend on the complexity of this dynamics (Dutkiewicz et al., 2013; Fu et al., 2016) and since there exists a large inter-model spread in NPP and EP among CMIP6 models (Kwiatkowski et al., 2020; Tagliabue et al., 2021). Furthermore, it would be useful to extend such simulations to, for example, 2300 to see whether the increased productivity of the small phytoplankton groups

are able to dampen the positive feedback, or whether they will also become more limited due to increasing stratification in the North Atlantic.

Appendix A Open Research

The Community Earth System Model v2 (CESM2) output can be downloaded from the Earth System Grid Federation (ESGF) (<https://esgf-node.llnl.gov/search/cmip6/>) (Danabasoglu, 2019). Processed datasets, scripts for plotting, and scripts related to the Simple Carbon Project Model (SCP-M) used for this study can be found at 10.5281/zenodo.6770132 (Boot et al., 2022). We have also included a list of datasets downloaded from the ESGF which are necessary to create the processed datasets, and the figures. The original SCP-M V1.0 can be found at 10.5281/zenodo.1310161 (C. M. O'Neill et al., 2018).

Acknowledgments

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