



## **Influence of High Temperature on Different Plankton Ecology in the Future Ocean: Modeling Approach**

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### ***Abstract***

To accurately predict the responses of marine ecosystems to climate change, it is imperative to comprehend the interaction between increased Carbon Dioxide (CO<sub>2</sub>) levels and elevated temperatures and how it affects marine plankton ecology. However, there is a limited number of studies that have investigated the impacts of increased CO<sub>2</sub> on marine plankton ecology. This study explores future ocean scenarios of global plankton dynamics under the influence of climate projections utilizing EcoGENIE, a simplified Earth system model that couples biogeochemistry, ocean circulation, and climate processes to simulate long-term global environmental changes. A significant decline in total carbon biomass is observed worldwide, particularly at higher latitudes, with a pronounced reduction in plankton biomass in the North Atlantic Ocean. Surprisingly, in the isolating phytoplankton experiments, an increase in plankton biomass is observed, contrasting with the coupled phytoplankton-zooplankton experiments. Surface alkalinity and Dissolved Inorganic Carbon (DIC) patterns is also predicted to increase in the model projections of the future global ocean, particularly in the Atlantic Ocean. While sea surface temperature rises due to elevated CO<sub>2</sub> emissions, phytoplankton play a role in mitigating the increase in alkalinity and DIC in the surface ocean. Examination of ocean circulation patterns, focusing on the weakened Atlantic Meridional Overturning Circulation, reveals a connection between plankton ecology and ocean circulation. Additional experiments suggest that if the CO<sub>2</sub> emissions will further increase, the impact on plankton biomass will persist and intensify, particularly in the Atlantic Ocean. This study emphasizes the intricate connection between changes in the ocean biogeochemical cycles, induced by climatic stresses, and the ecological dynamics of global planktonic communities.

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**Keywords:** Climate Change, Plankton Ecology, EcoGENIE Earth System Model, CO<sub>2</sub>

## Introduction

The plankton ecosystem, an important component of marine environments, encompasses diverse microscopic organisms such as phytoplankton and zooplankton, playing a pivotal role in nutrient cycling and supporting marine food webs (Botterell et al., 2023; Brierley, 2017; Jahan & Singh, 2023; Naselli-Flores & Padisák, 2022). Photosynthetic plankton is a fundamental support for nearly all ocean life, including fish stocks that offer essential nutrition to over half of the human population (Hollowed et al., 2013). Phytoplankton, as primary producers, form the foundation of marine food webs by converting inorganic carbon into organic matter through photosynthesis, thereby driving oceanic carbon cycling and oxygen production (Falkowski et al., 1998; Field et al., 1998). Zooplankton, in turn, serve as crucial intermediaries that transfer this energy to higher trophic levels and regulate phytoplankton populations through grazing, significantly influencing nutrient recycling and carbon export to the deep ocean (Calbet, 2001; Steinberg & Landry, 2017). Ecosystem modeling is important for studying the past and predicting the future dynamics of marine plankton ecology (Allen et al., 2025; Dutkiewicz, Hickman, et al., 2015; Follows et al., 2007; Le Quéré et al., 2005; Richardson & Schoeman, 2004). Many studies emphasize the importance of understanding variability in plankton biomass and the factors influencing growth or collapse, such as nutrient availability, seawater temperature, and ocean acidification, to better assess the resilience and responses of plankton ecosystems to ongoing and future climate changes (Behrenfeld et al., 2006; Dutkiewicz, Morris, et al., 2015; Follows et al., 2007; Mimi et al., 2024).

Climate change poses a considerable threat to the stability of plankton ecosystems by embodying a multifaceted combination of stressors, notably characterized by rising temperatures and heightened atmospheric Carbon Dioxide (CO<sub>2</sub>) levels (Hartmann et al., 2013). The future impact of climate change, accompanied by rising CO<sub>2</sub> levels and increasing temperatures, is anticipated to significantly alter the marine plankton ecosystem by disrupting the biogeochemical cycle of the ocean (A. K et al., 2023; Azani et al., 2021; Brierley & Kingsford, 2009). Shifts in nutrient availability, affecting plankton growth and composition may lead to some of these changes, as already suggested by recent studies (Henson et al., 2021; Kalloniati et al., 2023; Kumar et al., 2022; Zhou et al., 2024). Additional to that, altered oceanic conditions may influence the interactions

between phytoplankton and zooplankton, potentially cascading through the marine food web and impacting the overall ecosystem dynamics. Furthermore, the oceanic biological carbon pump is likely to be influenced by increased temperature due to its control over photosynthesis and respiration rates (Armstrong McKay et al., 2021).

With the advent of industrialization and increased human activities, particularly the burning of fossil fuels, there has been already a notable surge in CO<sub>2</sub> emissions. The Representative Concentration Pathway 8.5 (RCP8.5) scenario (IPCC, 2019; Riahi et al., 2011), often considered a high-emission trajectory, anticipates a substantial rise in future CO<sub>2</sub> emissions. Projections under RCP8.5 suggest a trajectory where atmospheric CO<sub>2</sub> concentrations could reach unprecedented levels, significantly surpassing those observed in the historical record (Hausfather & Peters, 2020; Schwalm et al., 2020). These escalating CO<sub>2</sub> emissions contribute significantly to ongoing concerns about climate change and its potential repercussions on the Earth's climate system and ecosystems.

Numerical models serve as valuable quantitative tools to examine and comprehend the connections among plankton biodiversity, biogeochemistry, and climate (Cossarini et al., 2024). Intermediate Complexity Earth System Models (EMICs) are commonly utilized for investigating both past and future climates, providing simulations of plankton behavior and their influence on biogeochemistry (Hülse et al., 2017). Carbon-centric iteration of the GENIE Earth system model of intermediate complexity, known as cGENIE has been proven effective in investigating the connections between marine ecology and climate across various timescales and periods (Armstrong McKay et al., 2021; Asselot, 2021; Asselot et al., 2021; Sadi et al., 2024; Wilson et al., 2018). The Earth system model incorporating marine ecology, EcoGENIE, proves its efficacy through a comparison of outcomes with climatological and seasonal observations, showing consistency with data at both global and local scales (Ward et al., 2018). Highlighted in studies by Armstrong McKay et al. (2021), Asselot et al. (2023) and Naidoo-Bagwell et al. (2023), EcoGENIE emerges as a sophisticated framework for marine ecology within the Earth system, which stands out for its advanced features in simulating complex interactions among marine organisms. These studies collectively emphasize the effectiveness of the model in replicating observed patterns and dynamics, further highlighted through its comparative examination with the biogeochemical version of cGENIE. It ultimately showcases uniform global distributions of essential elements in various model versions.

In particular, Naidoo-Bagwell et al. (2023) incorporated a diatom functional group into the cGENIE model, ensuring alignment with observations and improving the representation of dissolved oxygen distribution. Asselot et al. (2023) investigated the influence of phytoplankton light absorption on climate, and uncovered effects such as diminished biological carbon pumps, elevated surface chlorophyll-a levels, and changes in sea surface temperature and atmospheric conditions. Ying et al. (2023) enhanced EcoGENIE by incorporating symbiosis and spine traits into foraminifer functional types, improving global foraminiferal representations. Barrett et al. (2023) investigates the impact of the Palaeocene-Eocene Thermal Maximum on foraminiferal carbonate production, revealing warming-induced poleward migration and a greater influence of sea surface warming over ocean acidification. These studies collectively demonstrate that EcoGENIE effectively reproduces marine ecology dynamics in the context of climate change, corroborating that the incorporation of novel ecological components and consideration of environmental factors into the model provide valuable tools for predicting and assessing climate change impacts on marine ecosystems.

In this study, we used three different numerical configurations to simulate the future climate in the Earth system model cGENIE, focusing on size-structured characteristics-based communities of global plankton. We investigate important features of modeled plankton communities, including factors like plankton biomass, nutrient levels, and other quantities related to changes in CO<sub>2</sub> emissions, which directly affect the plankton community. We further compare these findings with historical results of plankton ecosystems from previous studies to highlight differences and to further explore how warming affects ocean circulation and, consequently, plankton ecology. Finally, the paper outlines methodological challenges and suggests perspective directions for future research in this area.

## **Materials and Methods**

cGENIE stands as an Earth System Model of Intermediate Complexity, featuring a modular structure that integrates diverse elements of the Earth system (van de Velde et al., 2021; Ward et al., 2018). This includes ocean circulation, biogeochemical cycling, ocean sediment, and ocean-atmosphere interactions, as well as the long-term geological cycling of carbon and various tracers (for example; Dissolved Inorganic Carbon (DIC), alkalinity, CO<sub>2</sub>) derived from the solid Earth (Ward et al., 2018). The cGENIE model (Vervoort et al., 2021; Ying, 2024) employed in this study operates without seasonal forcing and is applied on a 36×36 km (0.32° × 0.32°) equal-area horizontal grid. The grid consists of 10 km



increments in longitude, maintaining uniformity in the sine of latitude. This results in 3.2 km latitudinal increments at the equator, gradually increasing to 19.2 km in the highest latitude band. The vertical dimension of the ocean is represented by 8 z-coordinate levels, from skin surface to 5000 m depth (Ridgwell et al., 2007; Ridgwell & Hargreaves, 2007).

The BIOGEM component, constituting the biogeochemical model, oversees both air–sea gases exchanges and the alteration and distribution of biogeochemical tracers within the ocean, as outlined in Ridgwell et al. (2007). The biological pump is primarily powered by the parameterized absorption of nutrients in the surface ocean. This flux is then stoichiometrically transformed into biomass, which is subsequently divided into dissolved or particulate organic matter for subsequent transport, sinking, and remineralization.

Trait-based models of plankton ecosystems, founded on fundamental ecological and physiological principles, provide a means to investigate the interplay among plankton ecosystems, biogeochemistry, and climate in a significantly altered, future Earth system compared to the present day (Negrete-García et al., 2022). Here, we employed an Earth system model that incorporates size-structured trait-based plankton communities to project the future state of plankton ecosystems under changing climate conditions. The plankton community is explicitly resolved in the standard ecological model known as EcoGENIE (Ward et al., 2018). EcoGENIE distinguishes various plankton populations based on functional groups (phytoplankton and zooplankton) and organism size (equivalent spherical diameter). Each population is linked to biomass state variables representing carbon, phosphorus, and chlorophyll-a.

In this model, the grazing behavior of zooplankton relies on the concentration of accessible prey biomass, featuring a maximum grazing rate dependent on size. The abundance of prey biomass is calculated as a lognormal function based on zooplankton-to-phytoplankton size ratios, where zooplankton predominantly feed on prey ten times smaller in equivalent spherical diameter. Ward et al. (2018) proved its preference, due to the smaller prey being less likely to escape and easier to ingest.

In this study, the Ecogem model was employed to simulate three distinct plankton groups denoted as NPD, 3P3Z, and 8P8Z. These labels correspond to different compositions of phytoplankton and zooplankton within each group. These specifically represent one phytoplankton without zooplankton, three

phytoplankton and three zooplankton, and eight phytoplankton and eight zooplankton, respectively. Two sets of CO<sub>2</sub> emission forces were applied in the simulation scenarios. The first spanned from 1765 to 2010, encompassing 245 years and utilizing historical CO<sub>2</sub> emissions forcing. The second set of emissions, adopting RCP8.5 CO<sub>2</sub> emission forcing, covered a 90-year period from 2010 to 2100. The objective of this investigation was to observe and analyze potential changes in the plankton community dynamics across the specified time frames for each plankton group under the influence of the two distinct CO<sub>2</sub> emission scenarios. Moreover, a long-term simulation extending from 2010 to 2500 under the RCP8.5 forcing scenario was conducted using the 8P8Z plankton configuration. This additional run aimed to capture the prolonged trajectory of oceanic and ecological changes beyond 2100, simulating how continuous CO<sub>2</sub> accumulation and associated warming might influence plankton biomass distribution, nutrient cycling, and ocean circulation on multi-century timescales.

Plankton Group	Phytoplankton	Zooplankton
NPD	1	0
3P3Z	3	3
8P8Z	8	8

Table 1: Composition of Plankton Functional Groups Used in the EcoGENIE Simulations

Time Period	CO2 Forcing Type	Duration
1765 – 2010	Historical	245 Years
2010 – 2100	RCP8.5	90 Years
2010 – 2500	RCP8.5	490 Years

Table 2: Description of CO<sub>2</sub> Forcing Scenarios Applied in the EcoGENIE Simulations

Results and Discussion

With an increase in the global ocean temperature, the impact on plankton biomass becomes apparent, showing varied responses in different regions of the world ocean. The analysis of future ocean scenarios, as illustrated in Figure 1, brings attention to a substantial decline in total carbon biomass compared to historical conditions, particularly evident in higher latitudes (Figure 1c).

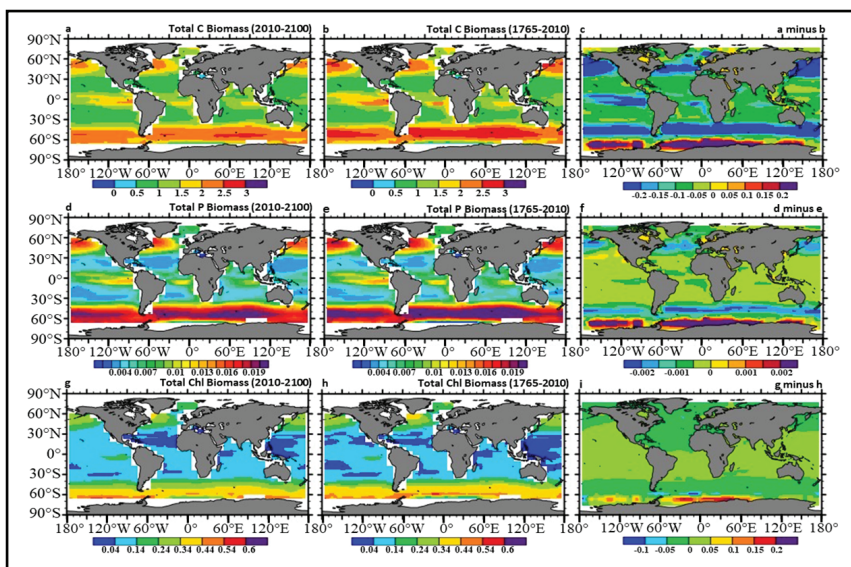


Figure 1: Model Projections of Global Plankton Communities in the Future Ocean Compared to Historical Experiments. Panels (a) and (b) Depict the Total Carbon Biomass (mmolCm-3) for the RCP8.5 and Historical Forcing Scenarios, Respectively. Panel (c) Illustrates the Difference Between the Two (a – b). Panels (d) and (e) Show the Total Phosphate Biomass (mmolPm-3), While Panel (f) Represents Their Difference (d – e). Finally, Panels (g) and (h) Display the Total Chlorophyll-a Biomass (mgChlm-3), and Panel (i) Illustrates the Difference Between Them (g – h) for the 8P8Z Simulation

Notably, this reduction is more pronounced in the North Atlantic, aligning with patterns observed in the 3P3Z community (refer to Figure 2). Interestingly, a distinct trend emerges when focusing solely on phytoplankton experiments, where both historical and RCP8.5 scenarios show an unexpected increase in phytoplankton biomass, presenting a counterintuitive outcome compared to the coupled phytoplankton-zooplankton experiments conducted (Figure 2). To substantiate the observed decline in biomass depicted in Figures 1 and 2, our investigation delves into the surface alkalinity and DIC patterns, revealing similar increases in the future ocean compared to the historical ocean (Figures 3c and 3f). Notably, the Atlantic Ocean exhibits a significant rise in both alkalinity and DIC in the future ocean, as evident in Figures 3a and 3d. Concurrently, higher Sea Surface Temperatures (SST) are observed in the future ocean due to elevated CO<sub>2</sub> emissions (Figure 3). However, an examination of Figure 4, focusing solely on phytoplankton, reveals that the differences in surface alkalinity and DIC are notably smaller than those presented in Figure 3. This suggests that phytoplankton

play a role in mitigating the increase in alkalinity and DIC in the surface ocean. While phytoplankton may not directly influence SST, their ability to sequester inorganic carbon through photosynthesis contributes to a mitigated impact on surface alkalinity and DIC's distributions of the surface ocean.

To gain a comprehensive understanding of the future ocean scenario, our investigation expands to encompass the ocean circulation pattern, particularly focusing on the Atlantic Ocean (Mimi & Liu, 2024). The examination reveals anomalies in the barotropic streamfunction in the North Atlantic, as illustrated in Figure 5c. Additionally, the vertical section of the global streamfunction emphasizes a more pronounced difference in transport (greater negative anomalies) between the future and historical scenarios in the northern hemisphere (Figure 5f). Furthermore, a specific emphasis on the North Atlantic (Figure 5i) corroborates findings from Figures 3 and 4, aligning with the observed patterns in surface alkalinity, DIC, and plankton dynamics of Figures 3 and 4. The weakened Atlantic Meridional Overturning Circulation is likely to be a key factor influencing the plankton community in the future Atlantic Ocean, and potentially on a global scale (Boot et al., 2025; Pontes & Menviel, 2024). Consequently, this result suggests a nuanced interconnection between plankton ecology and ocean circulation. To comprehensively assess whether changes in plankton community biomass are confined to the North Atlantic or extend to other oceanic regions, we use the output of the additional experiment ran with the 8P8Z model. This simulation spanned a duration of 490 years, from 2010 to 2500, incorporating RCP8.5 forcing (Figure 6).

As anticipated, the repercussions of elevated temperatures on the planktonic community extended equatorward from the North Atlantic (Figures 6c, f and i). Consequently, our findings suggest that as CO<sub>2</sub> emissions continue to rise, the impact on plankton biomass will persist and intensify, with the Atlantic Ocean experiencing a particularly heightened effect in the envisioned future scenario. Anthropogenic emissions of CO<sub>2</sub> leading to ocean acidification and carbonation have demonstrated impacts on diverse marine organisms, with potential implications for altering ecosystem functioning. In the natural environment, phytoplankton rely predominantly on CO<sub>2</sub> as the primary source of inorganic carbon for their growth. This is evidenced by the stable carbon isotope compositions of phytoplankton, which exhibit a pronounced inverse correlation with ambient CO<sub>2</sub> concentrations. Additionally, elevated values of stable carbon isotopes observed during diatom blooms suggest a limitation of photosynthesis rates due to diffusive CO<sub>2</sub> transport (Riebesell et al., 1993).

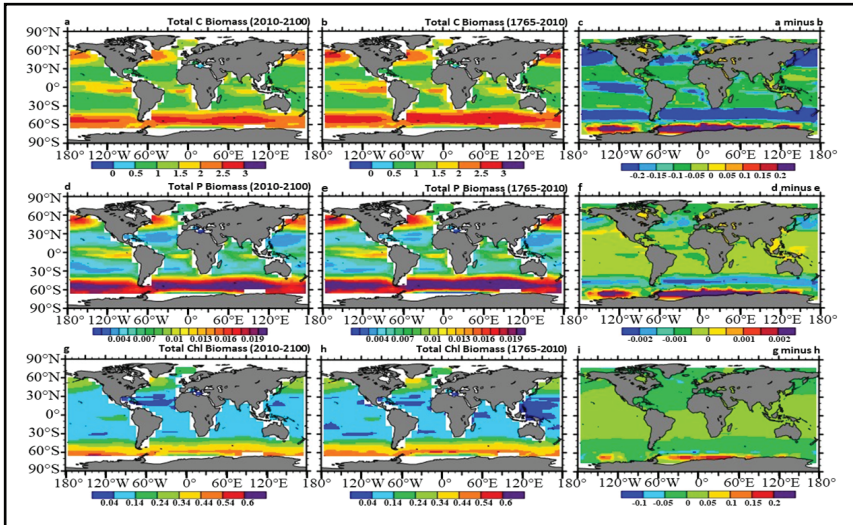


Figure 2: Same as Figure 1 but for the 3P3Z Simulation

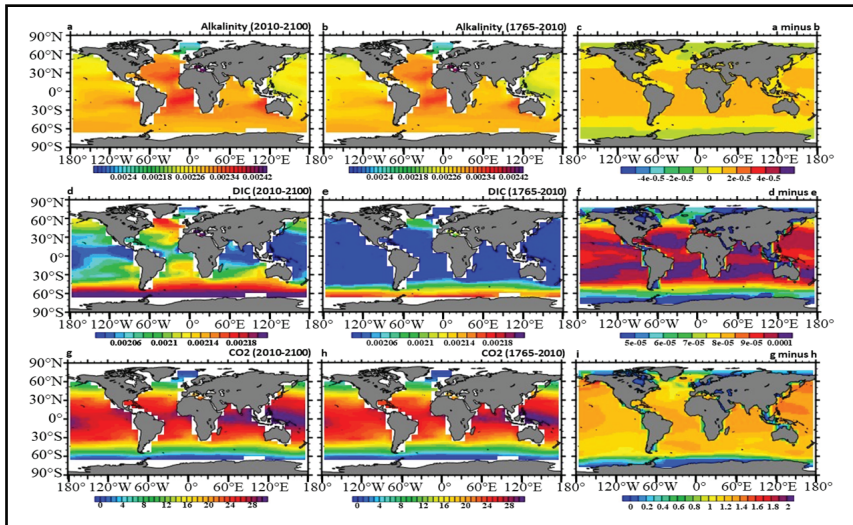


Figure 3: Model Projections of Surface Ocean Properties for Global Plankton Communities in the Future Ocean Compared to Historical Experiments. Panels (a) and (b) Show Surface Water Alkalinity (mol kg<sup>-1</sup>) for the RCP8.5 and Historical Forcing Scenarios, Respectively, While Panel (c) Illustrates the Difference Between Them (a – b). Panels (d) and (e) Present Dissolved Inorganic Carbon (mol kg<sup>-1</sup>), with Panel (f) Showing the Corresponding Difference (d – e). Finally, Panels (g) and (h) Display Sea Surface Temperature (°C), and Panel (i) Illustrates the Difference (g – h) for the 8P8Z Simulation



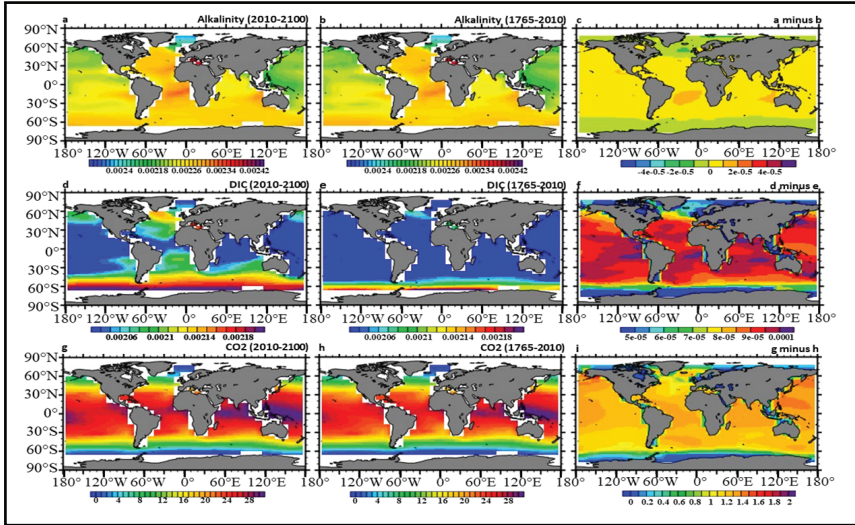


Figure 4: Same as Figure 3 but for the NPD Simulation

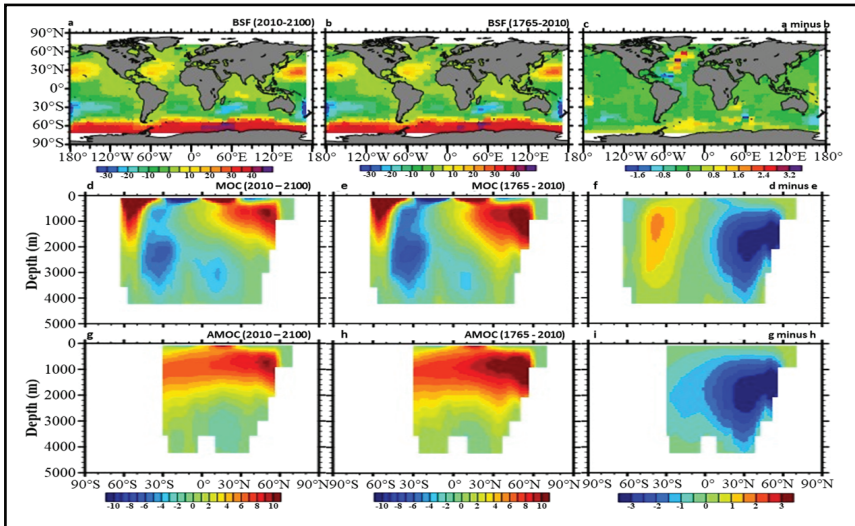


Figure 5: Model Projections of Ocean Circulation Patterns in the Future Ocean Compared to Historical Experiments. Panels (a) and (b) Display the Barotropic Streamfunction ( $S_v$ ) for the RCP8.5 and Historical Forcing Scenarios, Respectively, While Panel (c) Illustrates the Difference Between Them ( $a - b$ ). Panels (d) and (e) Show the Transport of the Global Overturning Circulation (MOC,  $S_v$ ), with Panel (f) Depicting the Difference ( $d - e$ ). Finally, Panels (g) and (h) Present the Atlantic Meridional Overturning Circulation Transport (AMOC,  $S_v$ ), and Panel (i) Illustrates the Difference ( $g - h$ ) for the 8P8Z Simulation

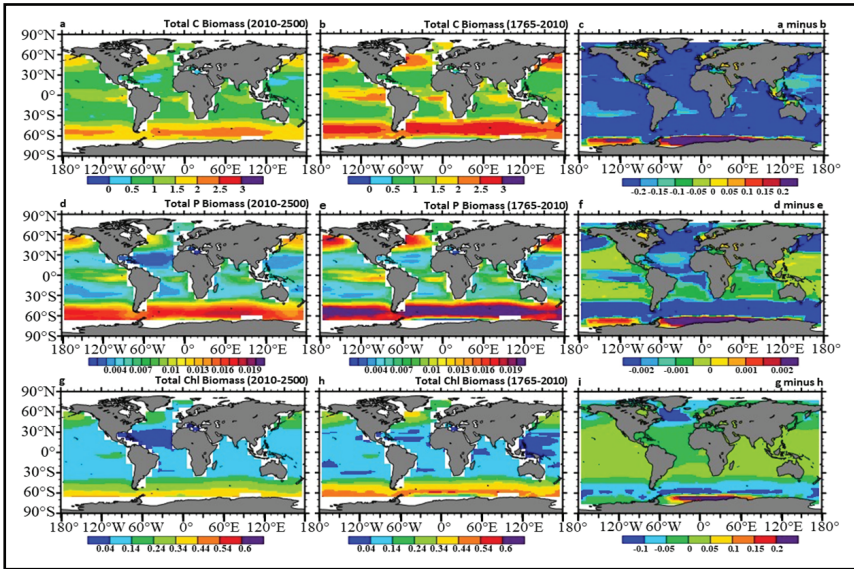


Figure 6: Same as Figure 1 but for the Simulation Encompassing the RCP8.5 Forcing Over 2010-2500

Elevated atmospheric CO<sub>2</sub> levels have resulted in increased concentrations of CO<sub>2</sub> in the oceans, offering enhanced carbon availability to marine primary producers (Huang et al., 2018). This increased carbon availability has the potential to alter the nutrient stoichiometry of these producers, leading to higher carbon-to-nutrient ratios. Consequently, the quality of primary producers as food for herbivores may undergo some changes. Their suitability as food for herbivorous consumers may have affected by the elevated presence of CO<sub>2</sub> accessible to primary producers. The increased carbon availability has the potential to alter the nutrient balance in primary producers, potentially leading to constraints in other essential nutrients (nitrogen and phosphorus). Unlike exhibiting nutrient composition homeostasis, primary producers mirror the nutrient composition of their surroundings. Therefore, when CO<sub>2</sub> availability is heightened, an expectation of higher carbon-to-nutrient ratios is foreseen, as indicated by several studies (Crichton et al., 2021; Schoo et al., 2013; and van de Velde et al., 2021).

This study significantly contributes to understanding marine ecosystem dynamics under climate change, aligning with key aspects in the field (for example; ocean modeling, ecosystem dynamics). It emphasizes the pivotal role of zooplankton in phytoplankton primary production, in harmony with the



investigation of the impacts of increased CO<sub>2</sub> and temperature on marine plankton ecology (Algueró-Muñiz et al., 2019; Steinberg & Landry, 2017). Concurrently, our findings are consistent with the ones of Kléparski et al. (2023) on phenological shifts in phytoplankton, particularly in the North Atlantic, further supporting the observed decline in total carbon biomass and emphasizing implications for broader plankton dynamics and carbon export. Additionally, simulations by Dupont et al. (2023) support our additional experiments, confirming a persisting impact on plankton biomass, especially in the Atlantic Ocean, under rising CO<sub>2</sub> emissions. Furthermore, our results agree with the ones of Kim et al. (2023) on the fact that the worldwide decrease in bacterial carbon biomass underscores the intricate connections between phytoplankton and oceanographic shifts, such as global circulation. Seifert et al. (2023)'s exploration of dual driver interactions – simultaneous climate stressors, such as temperature rise and CO<sub>2</sub> induced acidification, whose interactive effects can produce complex, non-linear responses in plankton communities – also suggested nuanced impacts on various planktonic components. Elsworth et al. (2023) provided insight into decreased variability in global phytoplankton carbon biomass, resonating with the long-term consequences of rising CO<sub>2</sub> emissions. Notably, Kwon et al. (2022) demonstrated that phosphorus utilization corresponds with an unexpected increase in phytoplankton biomass. Additionally, findings of Henson et al. (2021) on increased turnover in the phytoplankton community supported the observed shifts, emphasizing long-term ecological considerations. Lotterhos et al. (2021) highlighted the importance of understanding the regional effects of global novelty impacts on plankton biomass in the Atlantic Ocean. Raven & Beardall (2021) emphasized ocean acidification, highlighting the need for multifactorial experiments. CGENIE is an Earth System Model of Intermediate Complexity (EMIC), uses highly parameterized and relatively coarse-resolution ocean circulation and its simplification limits the ability to capture regional variations. Despite recognizing CGENIE model limitations, the study effectively underscores the intricate interconnection between climate driven ocean changes and plankton ecology, making a valuable contribution to comprehending marine ecosystem responses to ongoing climate change challenges.

## Conclusion

This study investigated the projected impacts of rising atmospheric CO<sub>2</sub> concentrations and increasing ocean temperatures on global plankton dynamics using an earth system model, the EcoGENIE model. By integrating ocean circulation, biogeochemistry, and ecological interactions, the model provided valuable insights into how future climate change may reshape marine plankton ecosystems.

Our simulations revealed a substantial global decline in total carbon biomass, particularly at higher latitudes and within the North Atlantic Ocean, highlighting the vulnerability of these regions to climatic stressors. Notably, when phytoplankton were modeled in isolation, their biomass showed an increase, suggesting that interactions with zooplankton play a crucial role in regulating primary productivity. Furthermore, the model projected significant rises in surface alkalinity and DIC, especially across the Atlantic, while phytoplankton activity appeared to mitigate these effects through carbon sequestration. Ocean circulation analysis also indicated a weakening of the Atlantic Meridional Overturning Circulation, underscoring its close link to primary productivity and plankton distribution.

Our study emphasizes the potential impacts on marine organisms, with phytoplankton adapting to elevated CO<sub>2</sub> levels. However, it is important to recognize the limitations of the CGENIE model, as it restricts the detailed representation of complex ecological interactions, especially on regional scale. Additionally, simulation inputs should ideally be derived from primary data sources (CTD or Argo derived) to produce more realistic outcomes. Future studies are encouraged to employ more advanced models (ROMS coupled with NPZD, Delft3D-WQ etc.) and integrate multidisciplinary approaches to deepen our understanding of the intricate connections between oceanic processes and plankton dynamics under the pressures of climate change.

Overall, this study advances our understanding of how climate-driven alterations in ocean chemistry and circulation could transform plankton ecology, a foundational component of marine food webs and global carbon cycling. Strengthening predictive modeling efforts will be essential for anticipating ecosystem responses and guiding sustainable management strategies in a rapidly changing ocean.

## References

- Priya A. K, P., M., Rajamanickam, S., Sivarethinamohan, S., Gaddam, M. K. R., Velusamy, P., R., G., Ravindiran, G., Gurugubelli, T. R., & Muniasamy, S. K. (2023). Impact of climate change and anthropogenic activities on aquatic ecosystem – A review. *Environmental Research*, 238, 117233. <https://doi.org/10.1016/J.ENVRES.2023.117233>
- Algueró-Muñiz, M., Horn, H. G., Alvarez-Fernandez, S., Spisla, C., Aberle, N., Bach, L. T., Guan, W., Achterberg, E. P., Riebesell, U., & Boersma, M. (2019). Analyzing the impacts of elevated-CO<sub>2</sub> levels on the development of a subtropical zooplankton community during oligotrophic conditions and simulated upwelling. *Frontiers in Marine Science*, 6(FEB), 378598. <https://doi.org/10.3389/FMARS.2019.00061/TEXT>
- Allen, R. J., Lee, Y. C., Thomas, A., Duarte, D., Mimi, M. S., Li, K. Y., Wenzel, B., Jeon, J. G., & Clifton, O. E. (2025). Atmospheric chemistry enhances the climate mitigation potential of tree restoration. *Communications Earth and Environment*, 6(1), 1–16. <https://doi.org/10.1038/S43247-025-02343-9>
- Armstrong McKay, D. I., Cornell, S. E., Richardson, K., & Rockström, J. (2021). Resolving ecological feedbacks on the ocean carbon sink in Earth system models. *Earth System Dynamics*, 12(3), 797–818. <https://doi.org/10.5194/esd-12-797-2021>
- Asselot, R. (2021). The role of marine biota in the climate system-an Earth system model approach [Staats-und Universitätsbibliothek Hamburg Carl von Ossietzky]. <https://doi.org/10.13140/RG.2.2.13951.53928>
- Asselot, R., Lunkeit, F., Holden, P. B., & Hense, I. (2021). The relative importance of phytoplankton light absorption and ecosystem complexity in an Earth system model. *Journal of Advances in Modeling Earth Systems*, 13(5), e2020MS002110. <https://doi.org/10.1029/2020MS002110>
- Asselot, R., Lunkeit, F., Holden, P., & Hense, I. (2023). A missing link in the carbon cycle: phytoplankton light absorption under RCP scenarios. *EGUsphere*, 2023, 1–32. <https://doi.org/10.5194/egusphere-2023-921>
- Azani, N., Ghaffar, M. A., Suhaimi, H., Azra, M. N., Hassan, M. M., Jung, L. H., & Rasdi, N. W. (2021). The impacts of climate change on plankton as live food: A review. *IOP Conference Series: Earth and Environmental Science*, 869(1). <https://doi.org/10.1088/1755-1315/869/1/012005>
- Barrett, R., Adebawale, M., Birch, H., Wilson, J. D., & Schmidt, D. N. (2023).

Planktic foraminiferal resilience to environmental change associated with the PETM. *Paleoceanography and Paleoclimatology*, 38(8), e2022PA004534. <https://doi.org/10.1029/2022PA004534>

Behrenfeld, M. J., O'Malley, R. T., Siegel, D. A., McClain, C. R., Sarmiento, J. L., Feldman, G. C., Milligan, A. J., Falkowski, P. G., Letelier, R. M., & Boss, E. S. (2006). Climate-driven trends in contemporary ocean productivity. *Nature*, 444(7120), 752–755. <https://doi.org/10.1038/nature05317>

Boot, A. A., Steenbeek, J., Coll, M., von der Heydt, A. S., & Dijkstra, H. A. (2025). Global Marine Ecosystem Response to a Strong AMOC Weakening Under Low and High Future Emission Scenarios. *Earth's Future*, 13(1), e2024EF004741. <https://doi.org/10.1029/2024EF004741>

Botterell, Z. L. R., Lindeque, P. K., Thompson, R. C., & Beaumont, N. J. (2023). An assessment of the ecosystem services of marine zooplankton and the key threats to their provision. *Ecosystem Services*, 63, 101542. <https://doi.org/10.1016/J.ECOSER.2023.101542>

Brierley, A. S. (2017). Plankton. *Current Biology*, 27(11), R478–R483. <https://doi.org/10.1016/J.CUB.2017.02.045>

Brierley, A. S., & Kingsford, M. J. (2009). Impacts of Climate Change on Marine Organisms and Ecosystems. *Current Biology*, 19(14), R602–R614. <https://doi.org/10.1016/J.CUB.2009.05.046>

Calbet, A. (2001). Mesozooplankton grazing effect on primary production: A global comparative analysis in marine ecosystems. *Limnology and Oceanography*, 46(7), 1824–1830. <https://doi.org/10.4319/LO.2001.46.7.1824>

Cossarini, G., Moore, A., Ciavatta, S., & Fennel, K. (2024). Numerical Models for Monitoring and Forecasting Ocean Biogeochemistry: a short description of present status. <https://doi.org/10.5194/SP-2024-8>

Crichton, K. A., Ridgwell, A., Lunt, D. J., Farnsworth, A., & Pearson, P. N. (2021). Data-constrained assessment of ocean circulation changes since the middle Miocene in an Earth system model. *Climate of the Past*, 17(5), 2223–2254. <https://doi.org/10.5194/cp-17-2223-2021>

Dupont, L., Le Mézo, P., Aumont, O., Bopp, L., Clerc, C., Ethé, C., & Maury, O. (2023). High trophic level feedbacks on global ocean carbon uptake and marine ecosystem dynamics under climate change. *Global Change Biology*, 29(6), 1545–1556. <https://doi.org/10.1111/gcb.16558>

Dutkiewicz, S., Hickman, A. E., Jahn, O., Gregg, W. W., Mouw, C. B., & Follows, M. J. (2015). Capturing optically important constituents and properties in a marine biogeochemical and ecosystem model. *Biogeosciences*, 12(14), 4447–4481. <https://doi.org/10.5194/bg-12-4447-2015>

Dutkiewicz, S., Morris, J. J., Follows, M. J., Scott, J., Levitan, O., Dyhrman, S. T., & Berman-Frank, I. (2015). Impact of ocean acidification on the structure of future phytoplankton communities. *Nature Climate Change*, 5(11), 1002–1006. <https://doi.org/10.1038/nclimate2722>

Elsworth, G. W., Lovenduski, N. S., Krumhardt, K. M., Marchitto, T. M., & Schlunegger, S. (2023). Anthropogenic climate change drives non-stationary phytoplankton internal variability. *Biogeosciences*, 20(21), 4477–4490. <https://doi.org/10.5194/bg-20-4477-2023>

Falkowski, P. G., Barber, R. T., & Smetacek, V. (1998). Biogeochemical Controls and Feedbacks on Ocean Primary Production. *Science*, 281(5374), 200–206. <https://doi.org/10.1126/SCIENCE.281.5374.200>

Field, C. B., Behrenfeld, M. J., Randerson, J. T., & Falkowski, P. (1998). Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science*, 281(5374), 237–240. <https://doi.org/10.1126/SCIENCE.281.5374.237>

Follows, M. J., Dutkiewicz, S., Grant, S., & Chisholm, S. W. (2007). Emergent biogeography of microbial communities in a model ocean. *Science*, 315(5820), 1843–1846. <https://doi.org/10.1126/science.1138544>

Hartmann, D. L., Tank, A., & Rusticucci, M. (2013). IPCC fifth assessment report, climate change 2013: The physical science basis. *Ipcc Ar5*, 5, 31–39.

Hausfather, Z., & Peters, G. P. (2020). RCP8.5 is a problematic scenario for near-term emissions. *Proceedings of the National Academy of Sciences of the United States of America*, 117(45), 27791–27792. <https://doi.org/10.1073/PNAS.2017124117>

Henson, S. A., Cael, B. B., Allen, S. R., & Dutkiewicz, S. (2021). Future phytoplankton diversity in a changing climate. *Nature Communications*, 12(1), 1–8. <https://doi.org/10.1038/S41467-021-25699-W>

Hollowed, A. B., Barange, M., Beamish, R. J., Brander, K., Cochrane, K., Drinkwater, K., Foreman, M. G. G., Hare, J. A., Holt, J., Ito, S., & Others. (2013). Projected impacts of climate change on marine fish and fisheries. *ICES Journal of Marine Science*, 70(5), 1023–1037. <https://doi.org/10.1093/icesjms/fst081>

- Huang, Y., Liu, X., Laws, E. A., Bingzhang, C., Li, Y., Xie, Y., Wu, Y., Gao, K., & Huang, B. (2018). Effects of increasing atmospheric CO<sub>2</sub> on the marine phytoplankton and bacterial metabolism during a bloom: A coastal mesocosm study. *Science of The Total Environment*, 633, 618–629. <https://doi.org/10.1016/J.SCITOTENV.2018.03.222>
- Hülse, D., Arndt, S., Wilson, J. D., Munhoven, G., & Ridgwell, A. (2017). Understanding the causes and consequences of past marine carbon cycling variability through models. *Earth-Science Reviews*, 171, 349–382. <https://doi.org/10.1016/j.earscirev.2017.06.004>
- IPCC. (2019). Summary for Policymakers. *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. [https://www.ipcc.ch/site/assets/uploads/sites/3/2019/11/03\\_SROCC\\_SPM\\_FINAL.pdf](https://www.ipcc.ch/site/assets/uploads/sites/3/2019/11/03_SROCC_SPM_FINAL.pdf)
- Jahan, S., & Singh, A. (2023). The Role of Phytoplanktons in the Environment and in Human Life, a Review. *Basrah Journal of Science*, 41(2), 392–411. <https://doi.org/10.29072/BASJS.20230212>
- Kalloniati, K., Christou, E. D., Kournopoulou, A., Gittings, J. A., Theodorou, I., Zervoudaki, S., & Raitsos, D. E. (2023). Long-term warming and human-induced plankton shifts at a coastal Eastern Mediterranean site. *Scientific Reports*, 13(1), 21068. <https://doi.org/10.1038/S41598-023-48254-7>
- Kim, H. H., Laufkötter, C., Lovato, T., Doney, S. C., & Ducklow, H. W. (2023). Projected 21st-century changes in marine heterotrophic bacteria under climate change. *Frontiers in Microbiology*, 14, 1049579. <https://doi.org/10.3389/fmicb.2023.1049579>
- Kléparski, L., Beaugrand, G., Edwards, M., & Ostle, C. (2023). Phytoplankton life strategies, phenological shifts and climate change in the North Atlantic Ocean from 1850-2100. *Global Change Biology*. <https://doi.org/10.1111/gcb.16709>
- Kumar, B. S. K., Bhaskararao, D., Krishna, P., Lakshmi, C. N. V., Surendra, T., & Krishna, R. M. (2022). Impact of nutrient concentration and composition on shifting of phytoplankton community in the coastal waters of the Bay of Bengal. *Regional Studies in Marine Science*, 51, 102228. <https://doi.org/10.1016/J.RSMA.2022.102228>
- Kwon, E. Y., Sreeush, M. G., Timmermann, A., Karl, D. M., Church, M. J., Lee, S.-S., & Yamaguchi, R. (2022). Nutrient uptake plasticity in phytoplankton sustains future ocean net primary production. *Science Advances*, 8(51), eadd2475. <https://doi.org/10.1126/sciadv.add2475>

- Le Quéré, C., Harrison, S. P., Prentice, I. C., Buitenhuis, E. T., Aumont, O., Bopp, L., Claustre, H., Cotrim Da Cunha, L., Geider, R., Giraud, X., Klaas, C., Kohfeld, K. E., Legendre, L., Manizza, M., Platt, T., Rivkin, R. B., Sathyendranath, S., Uitz, J., Watson, A. J., & Wolf-Gladrow, D. (2005). Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Global Change Biology*, 11(11), 2016–2040. <https://doi.org/10.1111/J.1365-2486.2005.1004.x>
- Lotterhos, K. E., Láruson, Á. J., & Jiang, L.-Q. (2021). Novel and disappearing climates in the global surface ocean from 1800 to 2100. *Scientific Reports*, 11(1), 15535. <https://doi.org/10.1038/s41598-021-94872-4>
- Mimi, M. S., Ahmed, M. K., Chowdhury, K. M. A., Chowdhury, M. N. S., & Moontahab, A. (2024). The influence of climate variability events on the mesoscale eddies in the Bay of Bengal. *Journal of Sea Research*, 201(October), 102532. <https://doi.org/10.1016/j.seares.2024.102532>
- Mimi, M. S., & Liu, W. (2024). Atlantic Meridional Overturning Circulation slowdown modulates wind-driven circulations in a warmer climate. *Communications Earth and Environment*, 5(1), 1–9. <https://doi.org/10.1038/S43247-024-01907-5>
- Naidoo-Bagwell, A. A., Monteiro, F. M., Hendry, K. R., Burgan, S., Wilson, J. D., Ward, B. A., Ridgwell, A., & Conley, D. J. (2023). A diatom extension to the cGENIE Earth system model--EcoGENIE 1.1. *EGUsphere*, 2023, 1–29. <https://doi.org/10.5194/egusphere-2022-1254>
- Naselli-Flores, L., & Padisák, J. (2022). Ecosystem services provided by marine and freshwater phytoplankton. *Hydrobiologia*, 850(12–13), 2691. <https://doi.org/10.1007/S10750-022-04795-Y>
- Negrete-García, G., Luo, J. Y., Long, M. C., Lindsay, K., Levy, M., & Barton, A. D. (2022). Plankton energy flows using a global size-structured and trait-based model. *Progress in Oceanography*, 209, 102898. <https://doi.org/10.1016/J.POCEAN.2022.102898>
- Pontes, G. M., & Menviel, L. (2024). Weakening of the Atlantic Meridional Overturning Circulation driven by subarctic freshening since the mid-twentieth century. *Nature Geoscience*, 17(12), 1291–1298. <https://doi.org/10.1038/S41561-024-01568-1>
- Raven, J. A., & Beardall, J. (2021). Influence of global environmental change on plankton. *Journal of Plankton Research*, 43(6), 779–800. <https://doi.org/10.1093/plankt/fbab075>



- Riahi, K., Rao, S., Krey, V., Cho, C., Chirkov, V., Fischer, G., Kindermann, G., Nakicenovic, N., & Rafaj, P. (2011). RCP 8.5-A scenario of comparatively high greenhouse gas emissions. *Climatic Change*, 109(1), 33–57. <https://doi.org/10.1007/S10584-011-0149-Y>
- Richardson, A. J., & Schoeman, D. S. (2004). Climate impact on plankton ecosystems in the Northeast Atlantic. *Science*, 305(5690), 1609–1612. <https://doi.org/10.1126/science.1100958>
- Ridgwell, A., & Hargreaves, J. C. (2007). Regulation of atmospheric CO<sub>2</sub> by deep-sea sediments in an Earth system model. *Global Biogeochemical Cycles*, 21(2). <https://doi.org/10.1029/2006GB002764>
- Ridgwell, A., Hargreaves, J. C., Edwards, N. R., Annan, J. D., Lenton, T. M., Marsh, R., Yool, A., & Watson, A. (2007). Marine geochemical data assimilation in an efficient Earth System Model of global biogeochemical cycling. *Biogeosciences*, 4(1), 87–104. <https://doi.org/10.5194/bg-4-87-2007>
- Riebesell, U., Wolf-Gladrow, D. A., & Smetacek, V. (1993). Carbon dioxide limitation of marine phytoplankton growth rates. *Nature*, 361(6409), 249–251. <https://doi.org/https://doi.org/10.1038/361249a0>
- Sadi, S. H., Chowdhury, K. M. A., Tasnim, J., Hoque, M. M., Shaheen, M. A. R., & Moontahab, A. (2024). Assessing the Water Quality and Its Influence on the Chlorophyll-a Concentration in the Karnaphuli River Estuary. *The Dhaka University Journal of Earth and Environmental Sciences*, 13(1), 91–104. <https://doi.org/10.3329/DUJEEES.V13I1.77579>
- Schoo, K. L., Malzahn, A. M., Krause, E., & Boersma, M. (2013). Increased carbon dioxide availability alters phytoplankton stoichiometry and affects carbon cycling and growth of a marine planktonic herbivore. *Marine Biology*, 160, 2145–2155. <https://doi.org/10.1007/s00227-012-2121-4>
- Schwalm, C. R., Glendon, S., & Duffy, P. B. (2020). RCP8.5 tracks cumulative CO<sub>2</sub> emissions. *Proceedings of the National Academy of Sciences of the United States of America*, 117(33), 19656. <https://doi.org/10.1073/PNAS.2007117117>
- Seifert, M., Nissen, C., Rost, B., Vogt, M., Völker, C., & Hauck, J. (2023). Interaction matters: Bottom-up driver interdependencies alter the projected response of phytoplankton communities to climate change. *Global Change Biology*. <https://doi.org/10.1111/gcb.16799>
- Steinberg, D. K., & Landry, M. R. (2017). Zooplankton and the Ocean Carbon

- Cycle. *Annual Review of Marine Science*, 9(1), 413–444. <https://doi.org/10.1146/ANNUREV-MARINE-010814-015924/1>
- van de Velde, S. J., Hülse, D., Reinhard, C. T., & Ridgwell, A. (2021). Iron and sulfur cycling in the cGENIE. muffin Earth system model (v0. 9.21). *Geoscientific Model Development*, 14(5), 2713–2745. <https://doi.org/10.5194/gmd-14-2713-2021>
- Vervoort, P., Kirtland Turner, S., Rochholz, F., & Ridgwell, A. (2021). Retracted: Earth System Model Analysis of How Astronomical Forcing Is Imprinted Onto the Marine Geological Record: The Role of the Inorganic (Carbonate) Carbon Cycle and Feedbacks. *Paleoceanography and Paleoclimatology*, 36(10), e2020PA004090. <https://doi.org/10.1029/2020PA004090>
- Ward, B. A., Wilson, J. D., Death, R. M., Monteiro, F. M., Yool, A., & Ridgwell, A. (2018). EcoGENIE 1.0: plankton ecology in the cGENIE Earth system model. *Geoscientific Model Development*, 11(10), 4241–4267. <https://doi.org/10.5194/gmd-11-4241-2018>
- Wilson, J. D., Monteiro, F. M., Schmidt, D. N., Ward, B. A., & Ridgwell, A. (2018). Linking marine plankton ecosystems and climate: a new modeling approach to the warm early Eocene climate. *Paleoceanography and Paleoclimatology*, 33(12), 1439–1452. <https://doi.org/10.1029/2018PA003374>
- Ying, R. (2024). cgeniepy: A Python package for analysing cGENIE Earth System Model output. *Journal of Open Source Software*, 9(101), 6762. <https://doi.org/10.21105/JOSS.06762>
- Ying, R., Monteiro, F. M., Wilson, J. D., & Schmidt, D. N. (2023). ForamEcoGENIE 2.0: incorporating symbiosis and spine traits into a trait-based global planktic foraminiferal model. *Geoscientific Model Development*, 16(3), 813–832. <https://doi.org/10.5194/gmd-16-813-2023>
- Zhou, L., Yang, X., Li, K., Xiang, C., Wu, Y., Huang, X., Huang, L., & Tan, Y. (2024). Regime shift in a coastal pelagic ecosystem with increasing human-induced nutrient inputs over decades. *Water Research*, 263, 122147. <https://doi.org/10.1016/J.WATRES.2024.122147>