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Key Points:

- Modulating phytoplankton and zooplankton Fe stoichiometry significantly affects the timing and amplitude of the bloom seasonal cycle in the Subantarctic Zone
- Adjustments align the chlorophyll seasonal cycle with observations and carbon biomass but have minimal impact on carbon export fluxes
- A substantial increase in dissolved organic carbon (DOC) is indicative of strong microbial recycling that hinders the transfer of surface carbon to the deep ocean

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

T. B. Mashifane,
thulwaneng@gmail.com

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Author Contributions:

Conceptualization: S. J. Thomalla

Data curation: T. B. Mashifane

Formal analysis: T. B. Mashifane,

A. Tagliabue, S. J. Thomalla

Funding acquisition: S. J. Thomalla

Investigation: T. B. Mashifane,

A. Tagliabue, S. J. Thomalla

Methodology: T. B. Mashifane,

A. Tagliabue

Project administration: S. J. Thomalla

Software: T. B. Mashifane

Supervision: A. Tagliabue, S. J. Thomalla

Validation: T. B. Mashifane

Visualization: T. B. Mashifane

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Trait-Based Adjustments: Key to Improving Model Representation of the Bloom Seasonal Cycle in the Subantarctic Zone

T. B. Mashifane¹ , A. Tagliabue² , and S. J. Thomalla^{1,3} 

¹Southern Ocean Carbon–Climate Observatory, CSIR, Cape Town, South Africa, ²Department of Earth, Ocean and Ecological Sciences, School of Environmental Sciences, University of Liverpool, Liverpool, UK, ³Marine and Antarctic Research Centre for Innovation and Sustainability, University of Cape Town, Cape Town, South Africa

Abstract Southern Ocean phytoplankton have unique traits that allow them to survive extreme environmental conditions of low iron, light, and temperature. These traits are not well represented in Earth System Models and may lead to misrepresentation of the bloom seasonal cycle in this critical oceanic region. This has implications for understanding the role of the biological carbon pump in driving ocean carbon uptake and storage. We conduct a sensitivity analysis using a 1D model in the Subantarctic Zone to identify (a) the most sensitive parameters for improving representation of the seasonal cycle and its mechanisms and (b) the impact of these changes on carbon export. Lowering the phytoplankton iron quota or increasing zooplankton iron stoichiometry and both improve the seasonal cycle timing and amplitude, aligning chlorophyll and carbon seasonal cycle. However, the resulting increases in bloom amplitude translates into minimal change in carbon export due to enhanced cycling through the dissolved organic carbon pool.

Plain Language Summary Southern Ocean (SO) phytoplankton have unique traits and adaptations for surviving factors such as iron (Fe) limitation, low light conditions, and extremely low temperatures. These traits are generally not well-represented in Earth System Models and may contribute to inaccuracies in depicting the timing and magnitude of the SO bloom seasonal cycle, and by expansion the role of the biological carbon pump (BCP). Accurate trait estimates reflecting these adaptations are essential for properly capturing the bloom seasonal cycle, as well as predicting the future of the BCP in this region. We ran a series of experiments using a biogeochemical model in the Subantarctic Zone, focusing on parameters associated with SO phytoplankton, and zooplankton. We found that reducing the assumed Fe requirements of phytoplankton or increasing zooplankton Fe requirements and both led to a more realistic seasonal cycle. Lowering phytoplankton Fe requirements aligns with well documented adaptations of SO phytoplankton to low light and Fe conditions, while increasing zooplankton Fe requirements decreases their biomass and enhances Fe recycling, with both adjustments allowing the bloom seasonal cycle to align with satellite observations. However in both instances, the seasonal increase in surface carbon does not translate into comparative increases in carbon exported to depth.

1. Introduction

The Southern Ocean (SO) functions as a significant heat and carbon sink and as such plays an important role in regulating global climate. It absorbs ~40% of the global ocean carbon dioxide (CO₂) and uptake ~75% of the excess heat generated by anthropogenic CO₂ emissions (Frölicher et al., 2015). Phytoplankton play a significant role in the carbon cycle through CO₂ uptake and export via the biological carbon pump (BCP) (Schlitzer, 2002), which can store carbon on climate relevant timescales (Rae et al., 2018). As such, quantifying the strength, efficiency, and sensitivity of the BCP to climate change is fundamental for predicting longer term changes in the global carbon cycle and the impact of continued anthropogenic perturbations on atmospheric CO₂ levels (Henson et al., 2011; Laufkötter et al., 2017). Despite its importance, Earth system models (ESM's) disagree on the projected response of global carbon production and export, highlighting gaps in our knowledge of this major carbon flux (e.g., Hauck et al., 2015; Henson et al., 2011; Manizza et al., 2010; Matsumoto et al., 2010; Steinacher et al., 2010). Given their importance in driving the BCP, significant efforts have been made to understand phytoplankton and their distribution patterns across the global ocean (McKiver et al., 2015). Decades of observational studies have focused on understanding their large-scale regional and seasonal patterns using in situ

Writing – original draft:

T. B. Mashifane, S. J. Thomalla

Writing – review & editing:

T. B. Mashifane, A. Tagliabue,
S. J. Thomalla

measurements from ship cruises (e.g., Gist et al., 2009; Kang et al., 2004), as well as ocean color satellite observations (Gregg et al., 2003; McClain, 2009). This understanding has been fundamental in parameterizing ESMs to represent key biogeochemical processes, helping to overcome data limitations and serving as a powerful tool to explore a wide range of scientific challenges (Bishop & Wood, 2009). Although ESMs are generally proficient at capturing the basic large-scale distribution patterns of phytoplankton (McKiver et al., 2015), their inability to accurately resolve the bloom timing and magnitude in the SO has been highlighted (e.g., Doney et al., 2009; Vichi & Masina, 2009). The seasonal cycle sets much of the environmental variability in the factors that drive phytoplankton production with annual blooms generally driven by seasonal adjustments in physico-chemical conditions such as water column mixing, light and nutrient availability that dictate the growing conditions for phytoplankton (Racault et al., 2012; Thomalla et al., 2011, 2023). The timing, magnitude and duration of seasonal blooms are crucial in determining the amount of biomass available for export to deeper ocean layers or for transfer through the marine food web (Barnes, 2018; Rogers et al., 2020). It is therefore crucial to accurately represent the seasonal cycle of phytoplankton in ESMs, particularly in key regions like the SO, where the BCP plays a significant role in driving carbon export and storage and where primary production sustains a rich and diverse food web.

SO phytoplankton have distinctive traits and adaptations, particularly in response to the three key environmental factors that limit primary productivity in the SO: low iron (Fe) supply, low temperatures, and low light (Boyd, 2002; Strzepek et al., 2011, 2012, 2019). Some of these traits and adaptations are unique to SO phytoplankton and include alterations to their physiological processes that reduce their Fe requirements under limiting conditions (Sunda et al., 1991; Sunda & Huntsman, 1995). For example, SO phytoplankton are able to adjust their photosynthetic apparatus, to modify their pigment composition, and to fine-tune their metabolic pathways in order to reduce their Fe requirements, allowing them to function more efficiently under low Fe and light conditions (Strzepek et al., 2019; Strzepek & Harrison, 2004). Some of these traits can be incorporated into models using parameters that capture key aspects of phytoplankton growth strategies in response to varying environmental conditions that dictate temperature, nutrient and light limitation (Aumont et al., 2015). These include: the initial slope (α) of the photosynthesis–irradiance (P–I) curve that represents the photosynthetic efficiency of phytoplankton under light-limiting conditions, with a steep slope reflecting an ability of SO phytoplankton to be more efficient under lower light conditions relative to species adapted to higher light environments (Thomalla, Kean, et al., 2017); the maximum photosynthetic rate ($P_{\max}$), which under nutrient and light replete conditions may be biased too low due to a temperature dependence that neglects phytoplankton adaptation to a cold SO; the maximum chlorophyll-to-carbon (Chl/C) ratio ($\theta_{\max}^{\text{Chl}}$), which reflects photophysiological acclimation strategies to low light (chlorophyll packaging), where higher ratios are anticipated in the low light conditions of SO notably in winter (Thomalla, Ogunkoya, et al., 2017); the minimum half-saturation constant for Fe uptake ($K_{\text{Fe}}^{\min}$) during photosynthesis and respiration, which is indicative of the efficiency of the Fe acquisition system (where low values denote a species that are well adapted to scavenging Fe at low concentrations) and finally, the phytoplankton Fe quota ($\theta^{\text{Fe,psu}}$), which represents how much Fe is in the photosynthetic unit (psu) (Aumont et al., 2015; Flynn & Hipkin, 1999; Geider et al., 1997), and reflects an assumed iron cost requirement for photosynthesis (with higher values implying higher Fe requirements and greater susceptibility to Fe limitation).

Chronic under-sampling of the SO relative to its Northern Hemisphere counterparts could contribute to a reliance on model parameterizations that are predominantly derived from fewer data sets (Holder & Gnanadesikan, 2023), which may not accurately reflect SO specific traits. These parameterizations are often applied globally, assuming uniformity in phytoplankton traits and processes across regions. As a result, key aspects of phytoplankton dynamics in the SO, including their physiological adaptations and ecological interactions, may be underrepresented in global ESMs, potentially introducing significant biases in model performance for this critical region, with important implications for expected climate driven trends (Anugerahanti & Tagliabue, 2024). Changes in phytoplankton phenology typically reflect alterations in ecosystem function that can be linked to climate change (Henson et al., 2018; Racault et al., 2012; Thomalla et al., 2023). This is because the seasonal cycle is the mode of variability that couples physical climate forcing mechanisms with ecosystem responses in primary production, diversity and carbon export (Monteiro et al., 2011). Accordingly, it is expected that long-term trends in SO phytoplankton will reflect changes in the seasonal cycle. It is therefore important to correctly capture the seasonal cycle in ESMs to improve our understanding of the ecosystem and for confidence in future climate projections.

Beyond phytoplankton, it is anticipated that other biological processes that influence carbon cycling—such as those involving zooplankton (Rohr et al., 2023), may similarly require regionally specific parameterizations in ESM's to more accurately capture the distinctive ecological dynamics of the SO. Indeed—Rohr et al. (2023) identified zooplankton grazing as the most important driver of uncertainty in carbon cycling. Limited representation of stoichiometric flexibility between zooplankton and their prey, especially under varying prey composition and quality, can also lead models to misrepresent carbon assimilation efficiency (Richon et al., 2020). These inaccuracies can, in turn, lead to a lack of consensus regarding the estimated strength and future direction of the BCP (Henson et al., 2022). Although variable phytoplankton Fe/C stoichiometry is represented in some models to account for varying nutrient concentrations, zooplankton stoichiometry is typically fixed (Aumont et al., 2015; Twining & Baines, 2013). To address this, we focus on the Fe stoichiometry in zooplankton ($\theta^{\text{Fe,zoo}}$), as a representation of the minimum Fe content zooplankton require relative to their biomass to sustain physiological functions and growth. Lower values indicate a capacity for zooplankton to maintain physiological function under low-Fe conditions (i.e., higher efficiency in Fe use), whereas higher values reflect greater Fe demand, potentially increasing vulnerability to Fe limitation.

What remains unclear is the extent to which variability in these traits (spanning phytoplankton and zooplankton) may influence SO model performance, in particular in the context of an improved representation of the seasonal cycle. In this study, we use an offline one-dimensional (1D) biogeochemical model (PISCES) configured in the Subantarctic Zone (SAZ) to conduct a sensitivity study for determining which of the key parameters identified above elicit a response most closely aligned with the seasonal cycle observed by satellites. The parameters that evoke changes to the seasonal cycle in the model that align with remote sensing observations of phenology are subsequently examined further to better understand the mechanisms behind the observed changes and ultimately to determine the implications that these alterations may have on carbon export.

2. Methodology

Version 4.0.6 of NEMO was coupled with PISCES-v2 in an offline configuration (Galí et al., 2022). The PISCES 1D (P1D) simulations were forced with dynamical fields from the NEMO-C1D configuration and glider mixed layer depth (MLD) for the simulation period, to correct for the known MLD issues in the SO as detailed in (Text S1.1–1.2 and Figure S1B in Supporting Information S1). Initial conditions were obtained from the CSIRO Atlas of Regional Seas 2009 (CARS2009; Ridgway et al., 2002) climatology with nutrient restoration in the surface (Aumont et al., 2015; Galí et al., 2022).

The internal cycling of Fe in this configuration represents the amount of Fe in the psu ($\theta^{\text{Fe,psu}}$) required for photosynthesis in the minimum iron quota equation ($\theta^{\text{Fe,I}}$) in $\mu\text{mol Fe (mol C)}^{-1}$:

$$\theta^{\text{Fe,I}}_{\text{min}} = \theta^{\text{Fe,psu}} \theta^{\text{Chl,I}} + \frac{1.21 \times 10^{-5} \times 14}{55.85 \times 7.625} L_N^{\text{P}} \times 1.5 + \frac{1.15 \times 10^{-4} \times 14}{55.85 \times 7.625} L_{\text{NO}_3}^{\text{P}}, \quad (1)$$

where the three terms correspond to photosynthesis, respiration and nitrate reduction, respectively. The parameters: $\theta^{\text{Chl,I}}$, L_N^{P} and $L_{\text{NO}_3}^{\text{P}}$ represent the phytoplankton Chl/C ratio (mg Chl (mgC)^{-1}), and the nitrogen limitation terms, respectively (Text S1.3 in Supporting Information S1; Aumont et al., 2015). This equation applies to both phytoplankton groups (nanophytoplankton and diatoms as denoted by I) modeled in PISCES (Aumont et al., 2015). The default value of the $\theta^{\text{Fe,psu}}$ parameter in PISCES is fixed at $28.65 \mu\text{mol Fe g (Chl)}^{-1}$ based on Flynn and Hipkin (1999). This value represents the assumed amount of Fe in the psu required for photosynthesis ($\mu\text{mol Fe g (Chl)}^{-1}$), and is distinct from the intracellular Fe/C ratio ($\theta^{\text{Fe,I}}$) (in $\mu\text{mol Fe (molC)}^{-1}$), which quantifies Fe content per unit carbon ($\mu\text{mol Fe (molC)}^{-1}$). Reducing this value in PISCES lowers the assumed Fe requirement, bringing it closer to what we know of SO phytoplankton. This adjustment allows us to examine how varying Fe quotas affect the bloom seasonal cycle and key aspects of phytoplankton and zooplankton dynamics in the SO.

The $\theta^{\text{Fe,zoo}}$ parameter in PISCES is coded into the growth efficiency equation (e^{Z}) as:

$$e^{\text{Z}} = \min \left(1, \frac{\sum I^{\theta^{\text{Fe,I}}} g^{\text{Z}}(I)}{\theta^{\text{N,C}} \sum I^{\text{e}^{\text{Z}}}(I)}, \frac{\sum I^{\theta^{\text{Fe,I}}} g^{\text{Z}}(I)}{\theta^{\text{Fe,zoo}} \sum I^{\text{e}^{\text{Z}}}(I)} \right), \quad (2)$$

$$e^Z = e_N^Z \min \left(e_{\max}^Z, (1 - \sigma^Z) \frac{\sum I^{\theta^{\text{Fe},1}} g^Z(I)}{\theta^{\text{Fe},\text{zoo}} \sum I^{g^Z(I)}} \right) \quad (3)$$

Where $\theta^{N,1}$, $\theta^{N,C}$, $\theta^{\text{Fe},1}$, g^Z , $e_{\min}^Z$, $e_{\max}^Z$ and σ^Z represent phytoplankton N/C ratio (mol N (mol C)⁻¹), N/C quota (mol N (mol C)⁻¹), phytoplankton Fe/C ratio (μmol Fe (mol C)⁻¹), grazing (mmol C m⁻³ d⁻¹), minimum and maximum growth efficiency and the non-assimilated fraction of phytoplankton, respectively (Text S1.3 in Supporting Information S1). The default value of $\theta^{\text{Fe},\text{zoo}}$ in PISCES is fixed at 10 μmol Fe (mol C)⁻¹. When phytoplankton Fe/C ratio exceeds zooplankton Fe/C ratio, a portion of the excess carbon is lost as DOC (Text S1.3 in Supporting Information S1). By adjusting the zooplankton Fe stoichiometry, we interrogate how food quality influences growth and grazing, and how these changes cascade to affect the bloom seasonal cycle.

2.1. PID Sensitivity Experiments

An initial sensitivity analysis interrogated the seasonal bloom response to adjustments in parameters associated with SO plankton traits in PISCES. The parameters were tuned by multiplying their initial values with incremental factors (0.25–2.00x) and the subsequent response on bloom amplitude and timing were interrogated. Two parameters were selected from the outcome of the sensitivity experiments ($\theta^{\text{Fe},\text{psu}}$ and $\theta^{\text{Fe},\text{zoo}}$) that generated adjustments in bloom phenology closely aligned with satellite observations. Subsequent experiments were then performed to determine the impact of varying these parameters on bloom phenology in the context of the 21-years Ocean Color Climate Change Initiative (OC-CCI) climatology from (1999–2020; <https://esa-oceancolour-cci.org>; Sathyendranath et al., 2019). The OC-CCI data preprocessing and phenology metrics (Brody et al., 2013; Nicholson et al., 2024; Thomalla et al., 2023) are detailed in Section 1.4 in Supporting Information S1. In addition, we examined the impact of varying both parameters ($\theta^{\text{Fe},\text{zoo}}$ and $\theta^{\text{Fe},\text{psu}}$) in combination using matrix experiments on phytoplankton and zooplankton dynamics: primary production, grazing, Fe uptake, Fe recycling and biomass.

Discrepancies in the timing and amplitude of the chlorophyll-*a* (chl*a*) seasonal cycle persist between the reference run and the OC-CCI climatology, despite the prescribed glider-derived MLD (Figure 1a). The OC-CCI climatology shows a summer peak in February (0.39 mg m⁻³; range = 0.37–0.48 mg m⁻³), whereas the reference run peaks in winter (June; 0.27 mg m⁻³). Model phytoplankton carbon biomass is also decoupled from chl*a*, peaking in December (Figure 1b), with a muted seasonal amplitude (55% compared to 90% in OC-CCI), indicating an overall suppressed seasonal cycle.

3. Results and Discussion

We tested which parameters would elicit a response in the seasonal cycle of chl*a* and align it with satellite observations (Figures 1c–1h). Sensitivity experiments show that when α , $P_{\max}$, $\theta_{\max}^{\text{chl}}$ and $K_{\text{Fe}}^{\min}$ were incrementally varied, they generated shifts in the timing of the bloom peak to occur between June and October, and they altered the amplitude of the bloom peak to both increase and decrease within a range of between 0.13 and 0.47 mg m⁻³ (Figures 1c–1f). However, only by reducing our assumption of how much Fe is in the psu (i.e., a 0.25 decrease in $\theta^{\text{Fe},\text{psu}}$) and increasing the Fe stoichiometry required by zooplankton (i.e., a 1.5 and 1.75 increase in $\theta^{\text{Fe},\text{zoo}}$), were we able to generate an alignment of the bloom peak timing (i.e., to peak within the January–March range observed in satellites) and amplitude (i.e., to fall within the OC-CCI peak range of 0.31–0.48 mg m⁻³) (Figures 1g and 1h). A decrease in $\theta^{\text{Fe},\text{psu}}$ from the default value of ~28.65 μmol Fe (g Chl)⁻¹ lowers the phytoplankton Fe demand with intracellular Fe/C ratios to be more in line with what we understand to be true of SO phytoplankton (range = 0.29–71.9 μmol Fe (mol C)⁻¹), Table S2 in Supporting Information S1 (Hassler & Schoemann, 2009; Hawco et al., 2022; Strzepek et al., 2011, 2012, 2019; Sunda & Huntsman, 2011; Twining et al., 2004; Wang et al., 2020), as opposed to phytoplankton species from other oceanic regions with a much higher upper limit (range = 2.8–248.3 μmol Fe (mol C)⁻¹, Table S2 in Supporting Information S1) (Kustka et al., 2003; Lane et al., 2009; Marchetti et al., 2006; Taylor et al., 2013).

From a zooplankton perspective, an alignment of the bloom seasonal cycle in both timing and amplitude suggests the need for a higher $\theta^{\text{Fe},\text{zoo}}$ in this region. While PISCES is able to simulate variable phytoplankton Fe stoichiometry up to 80 μmol Fe (mol C)⁻¹ (Aumont et al., 2015; Twining & Baines, 2013), the default $\theta^{\text{Fe},\text{zoo}}$ in PISCES is fixed at 10 μmol Fe (mol C)⁻¹ for both meso- and microzooplankton. Fe stoichiometry and metabolic

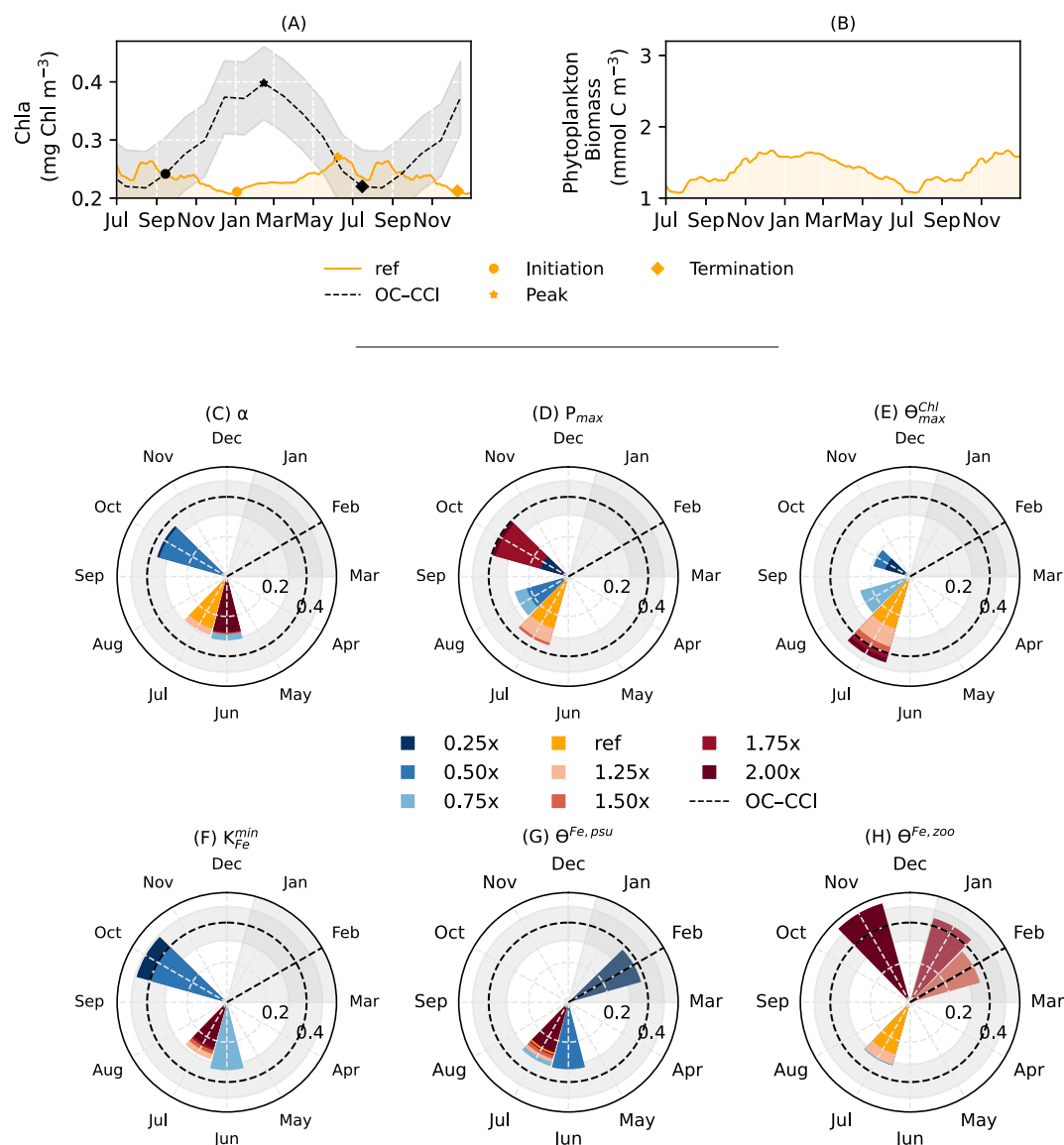


Figure 1. Top panel: time series of (a) chl a concentrations for the reference experiment and OC-CCI and (b) phytoplankton carbon biomass for the reference experiment. Shading on the OC-CCI time series represents the standard deviation. Bottom panel: experimental increments (0.25x, 0.5x, 0.75x, reference, 1.25x, 1.50x, 1.75x and 2.00x) of (c) α , (d) P_{max} , (e) θ_{max}^{chl} , (f) K_{Fe}^{min} , (g) $\theta_{Fe,psu}$ and (h) $\theta_{Fe,zoo}$ in P1D. Colored wedges represent the bloom amplitude (mg m⁻³) and timing of the peak within the surface 50 m for each model experiment. Dashed lines represent the climatological mean bloom peak timing (February) and amplitude (0.39 mg m⁻³) from the OC-CCI data set (1999–2020) with the gray shading reflecting the range in bloom peak timing (January–March) and amplitude (0.37–0.48 mg m⁻³).

demands are however known to vary according to size, age, sex, species and zooplankton diet (Baines et al., 2016; Chen et al., 2011, 2014; Sterner & Elser, 2002). For example, observations indicate that different species of Antarctic krill have an Fe stoichiometry that can range between 4 and 69 $\mu\text{mol Fe (mol C)}^{-1}$ (Ratnarajah et al., 2014). Some copepod species have also been shown to increase their Fe stoichiometry in response to an increase in food quality (Chen et al., 2014). Our results point to a possible mismatch between the variable phytoplankton Fe stoichiometry in PISCES and the fixed $\theta_{Fe,zoo}$. In this context, our results suggest that increasing the fixed $\theta_{Fe,zoo}$ value improves the alignment of the simulated bloom seasonal cycle with observations, likely by more realistically capturing how zooplankton adjust feeding and metabolic rates under improved food conditions.

3.1. Bloom Phenology Responses to Adjustments in Phytoplankton Fe Requirements and Zooplankton Fe Stoichiometry

Results from the matrix experiments (Figures 2a–2f) reveal how bloom phenology varies (in both timing and amplitude) in response to either adjustments in $\theta^{\text{Fe,psu}}$ and $\theta^{\text{Fe,zoo}}$ or both in relation to what is observed by satellites. The chl*a* seasonal cycle in the model is completely out of phase and in contrast with our knowledge of the SO bloom seasonal cycle which typically initiates in spring, peaks in summer and terminates in winter (Figure 2a; Thomalla et al., 2023). In addition, the seasonality of the reference run is muted relative to the OC–CCI climatology with a minimum to maximum range of ~ 0.21 – 0.27 mg m^{-3} (i.e., a 29% seasonal increase) when compared to satellite chl*a* that has similar minima but a climatological maximum that peaks at 0.39 mg m^{-3} (i.e., a 90% seasonal increase). This absence of a strong seasonal signal is similarly observed in the model reference run of phytoplankton carbon biomass. Moreover, the model reference runs suggest a decoupling between the seasonal cycle of chl*a* (Figure 2a) and phytoplankton carbon biomass (Figure 2b). This decoupling is indicative of a seasonal cycle in chlorophyll that does not reflect phytoplankton biomass, but rather a photophysiological response to light limitation that drives an increase in cellular chl*a* packaging in winter when MLD is at a maximum. Decreasing the phytoplankton Fe quota (Figure 2—blue) or increasing the zooplankton Fe stoichiometry (Figure 2—red) or adjusting both parameters in combination (Figure 2—green) aligns the phenology of the seasonal cycle of modeled chl*a* (with respect to both timing and amplitude) to be within the range of what is observed by satellites (red markers on the color bars of Figures 2c–2f). These adjustments also couple the seasonality of chl*a* to reflect that of phytoplankton biomass rather than photophysiology (Figure 2b). While a midway point of adjusting both parameters simultaneously ($\theta^{\text{Fe,psu}}_{1.375x}$, $\theta^{\text{Fe,zoo}}_{0.625x}$) similarly brings the bloom seasonal cycle into alignment (Figures 2a–2f).

3.2. Examining Bloom Phenology Adjustments in the Context of Primary Production, Grazing, Fe Uptake/Recycling, and Biomass

In this section we aim to better understand the mechanisms behind the seasonal alignment by interrogating the changes in modeled phenology when altering $\theta^{\text{Fe,zoo}}$ and/or $\theta^{\text{Fe,psu}}$ in the context of seasonal adjustments to phytoplankton primary production, zooplankton grazing, Fe uptake and recycling as well as biomass (of both phytoplankton and zooplankton) (Figures 3a–3f). It is clear from the seasonal cycle of the reference run with default $\theta^{\text{Fe,psu}}$ and $\theta^{\text{Fe,zoo}}$ (orange) that the high Fe demand of phytoplankton likely drives iron stress and dictates low phytoplankton Fe uptake rates (Figure 3c), which culminates in low rates of phytoplankton primary production (Figure 3a) and a depressed seasonal cycle in phytoplankton biomass (Figure 3e). Lowering the phytoplankton Fe requirements (blue line) to be more in line with what we know to be true of environmental adaptations of SO phytoplankton (Strzepek et al., 2011), increases primary production rates by 46% (Figure 3a) in summer for the same rate of Fe uptake $\sim 0.006 \mu\text{mol Fe m}^{-3} \text{ d}^{-1}$ (Figure 3c). Despite a small increase in grazing (Figure 3b), this increase in production with a decrease in $\theta^{\text{Fe,psu}}$ allows for a 47% increase in phytoplankton biomass relative to the reference run (Figure 3e).

Increasing the $\theta^{\text{Fe,zoo}}$ on the other hand (red line), increases the Fe requirements in zooplankton, therefore limiting their growth efficiency and decreasing their biomass by 26% (Figure 3f). This drives an increase in zooplankton Fe recycling $\sim 30\%$ (Figure 3d), which can be a significant contributor to uptake by phytoplankton (Richon et al., 2020). Increased zooplankton recycling extends the residence time of Fe in the surface ocean, which supports phytoplankton growth requirements (Boyd et al., 2012; Richon et al., 2020; Strzepek et al., 2005). This additional Fe availability drives a $\sim 40\%$ increase in summer phytoplankton Fe uptake (Figure 3c) and an associated 50% increase in carbon fixation (Figure 3a), which drives an 84% increase in summer phytoplankton biomass (Figure 3e). As expected the green line sits midway between the red and blue (Figures 3a–3h). The exception is for particulate organic carbon (POC) (Figure 3i) where the green line instead matches the reference run suggesting that adjusting both parameters in combination, in some instances, achieves the same effect as the reference.

3.3. Implications of the Adjustments for Carbon Export

Only a small fraction of the organic carbon fixed by primary production in the surface sunlit layers ultimately reaches the ocean interior (Steinberg et al., 2008). There is a complex interaction of processes that modify the fate of carbon impacting its export and transfer to depth (Henson et al., 2022). Here, we use the model runs to interrogate the impact on carbon export to the ocean interior when adjusting the $\theta^{\text{Fe,psu}}$ or $\theta^{\text{Fe,zoo}}$ parameters and

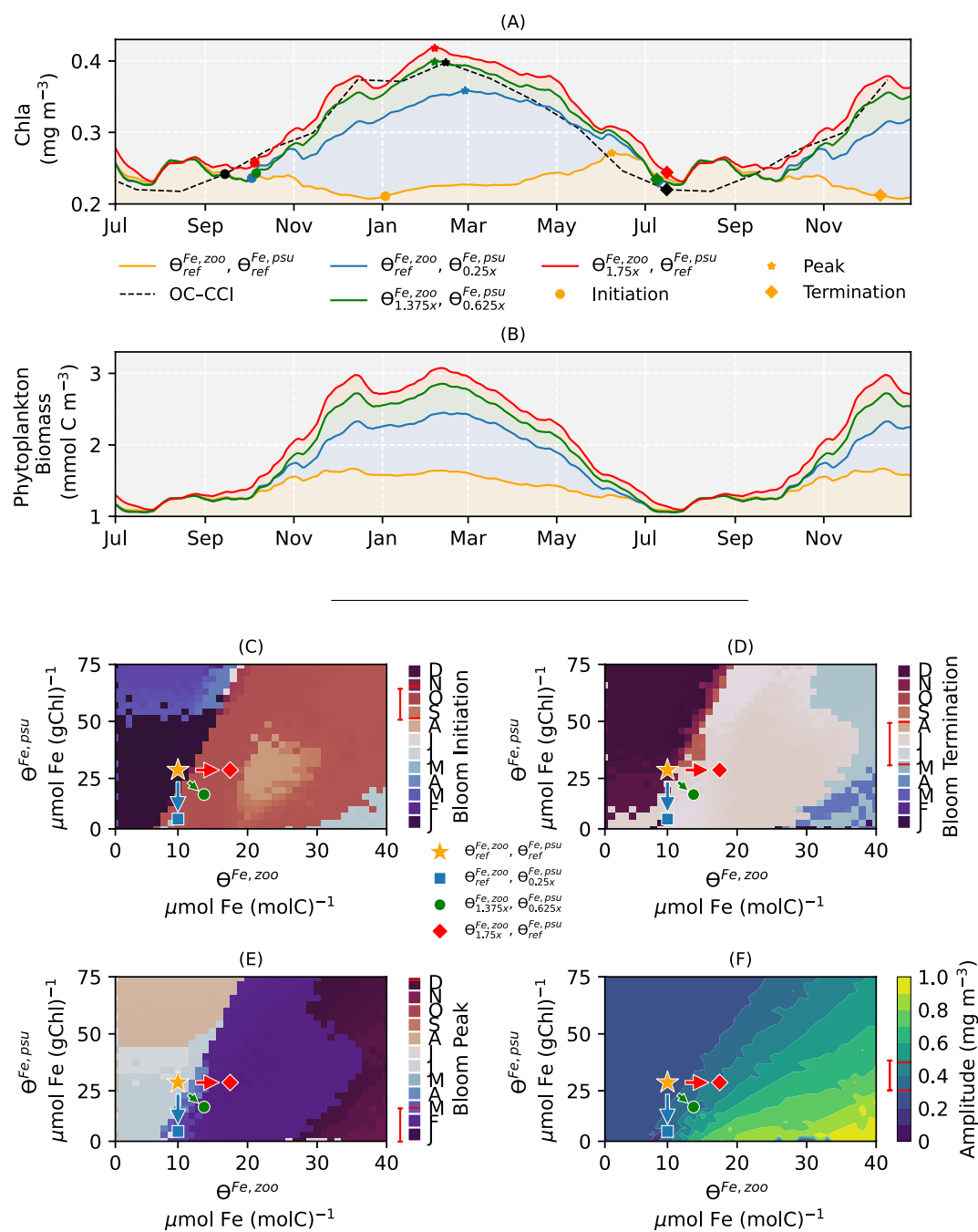


Figure 2. Top panel: seasonal cycle of mean (a) chl a (mg m^{-3}) for the experiments: reference (orange), $\theta_{0.25x}^{\text{Fe}, \text{psu}}$ (blue line), $\theta_{1.75x}^{\text{Fe}, \text{zoo}}$ (red line) and the OC-CCI data set (black dashed line) within the surface 50 m. Markers indicate the bloom initiation (circle), peak (star) and termination (diamond). (b) Phytoplankton carbon biomass (mmol C m^{-3}) for the reference (orange line), $\theta_{0.25x}^{\text{Fe}, \text{psu}}$ (blue line), and $\theta_{1.75x}^{\text{Fe}, \text{zoo}}$ (red line) experiments within the surface 50 m are also shown. Bottom panel: heat maps illustrating the relationship between $\theta_{\text{Fe}, \text{zoo}}$ and $\theta_{\text{Fe}, \text{psu}}$ on various bloom metrics are also shown: (c) bloom initiation, (d) timing of maxima, (e) termination and (f) amplitude (mg m^{-3}). Markers on the heatmaps represent the reference (orange) and responsive experiments ($\theta_{0.25x}^{\text{Fe}, \text{psu}}$ (blue) and ($\theta_{1.75x}^{\text{Fe}, \text{zoo}}$) (red)) and the mid-point of the two experiments in green ($\theta_{1.375x}^{\text{Fe}, \text{psu}}, \theta_{0.625x}^{\text{Fe}, \text{zoo}}$). Red lines on the amplitude colorbars indicate the OC-CCI range.

both to align the bloom seasonal cycle (in timing and amplitude) with observations. Despite major increases to the magnitude of the seasonal cycle of phytoplankton (47%–84% increases—Figure 3e) this does not translate into big differences in carbon export at 100 m. Indeed, there appears to be little to no difference in the amount of

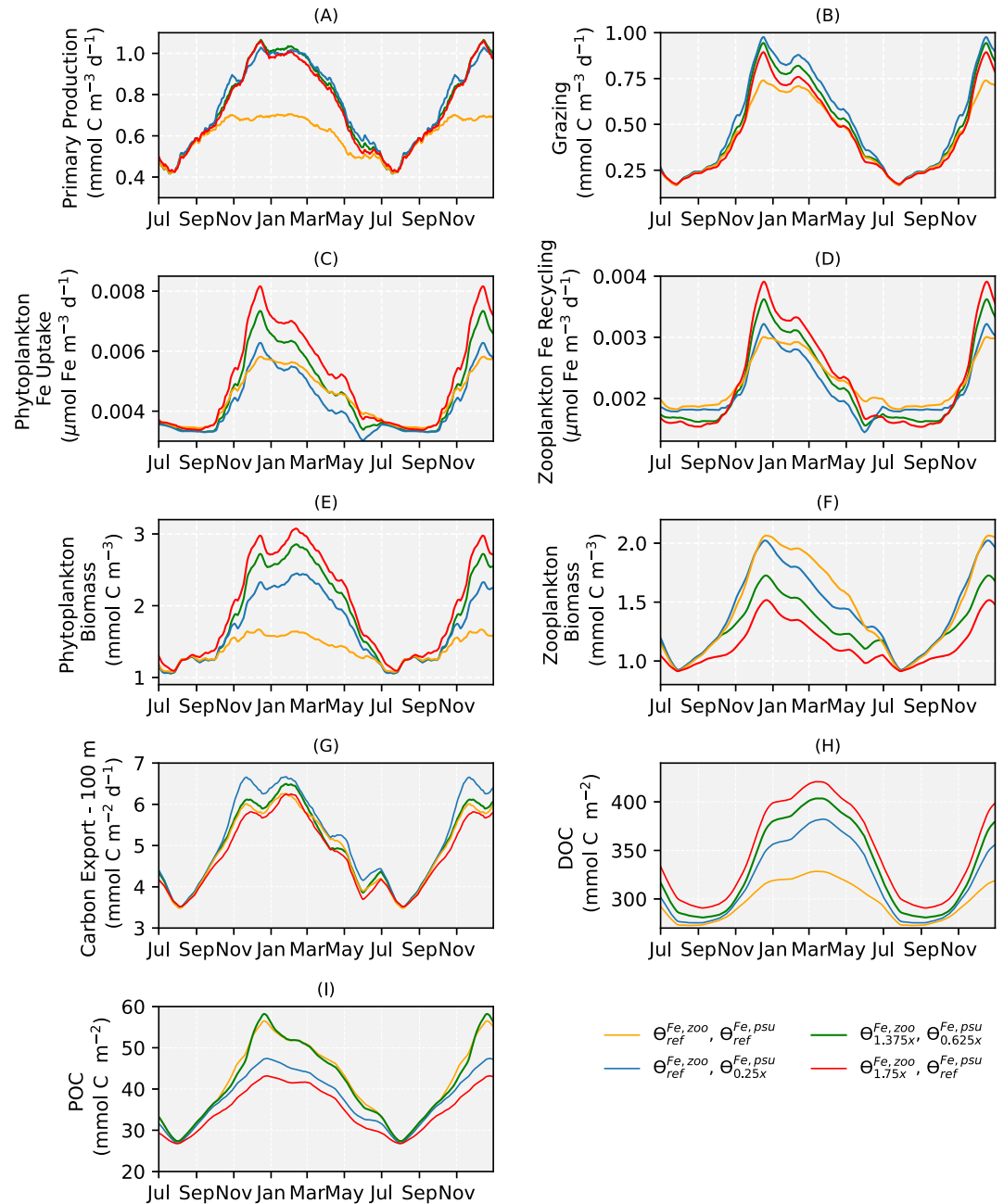


Figure 3. Seasonal cycle of mean (a) primary production ($\text{mmol C m}^{-3} \text{ d}^{-1}$), (b) grazing ($\text{mmol C m}^{-3} \text{ d}^{-1}$), (c) phytoplankton Fe uptake ($\mu\text{mol Fe m}^{-3} \text{ d}^{-1}$), (d) zooplankton Fe recycling ($\mu\text{mol Fe m}^{-3} \text{ d}^{-1}$), (e) phytoplankton biomass (mmol C m^{-3}) and (f) zooplankton biomass (mmol C m^{-3}) within the upper 50 m. Seasonal cycle of (g) carbon export at 100 m ($\text{mmol C m}^{-2} \text{ d}^{-1}$) and (h) dissolved organic carbon (mmol C m^{-2}) and (i) particulate organic carbon (mmol C m^{-2}) integrated over the top 100 m. The reference, and responsive experiments are represented by the reference (orange), blue ($\theta_{0.25x}^{\text{Fe,psu}}$), green ($\theta_{1.375x}^{\text{Fe,psu}}, \theta_{0.625x}^{\text{Fe,zoo}}$) and red ($\theta_{1.75x}^{\text{Fe,zoo}}$) lines, respectively.

carbon that is exported (when increasing $\theta^{\text{Fe,zoo}}$ or adjusting both in combination), and only a small increase in carbon export when lowering $\theta^{\text{Fe,psu}}$ (6.7%, Figure 3g). In either or both instances (and particularly the experiment where $\theta^{\text{Fe,zoo}}$ is increased), we see substantial increases in DOC and decreases in POC respectively, which is indicative of strong recycling (Figures 3h and 3i) that prevents the additional carbon being fixed during primary production from translating into export. In the model, when the phytoplankton Fe/C ratio exceeds zooplankton Fe stoichiometry, a fraction of the unassimilated carbon by zooplankton is lost as DOC. Henson et al. (2019)

proposed four regimes of export efficiency (which is the ratio between integrated primary production and carbon export at 100 m), which can be used to illuminate our model results. Here the reference run clearly falls into the regime of low productivity and relatively high export, which Henson et al. (2019) attribute to lower bacterial and mesozooplankton abundance where production and remineralization are decoupled such that a large fraction of the carbon being fixed during production can be exported. This seems to agree with the model where lower abundance of mesozooplankton and high POC account for low remineralization and low DOC under low primary production (Figures 3a–3h and 3i). On the other hand, our experimental runs (where $\theta^{\text{Fe,psu}}$ is decreased or $\theta^{\text{Fe,zoo}}$ is increased and both) fall into the high primary productivity—low export regime that is characterized by high productivity which is tightly coupled to strong surface recycling by zooplankton reducing the amount of carbon being exported (Henson et al., 2019; Le Moigne et al., 2016; Maiti et al., 2013).

Indeed, it is clear from the reference run that low primary productivity drives a depressed seasonal cycle (Figures 2a–2e orange line) that is dominated by smaller phytoplankton and zooplankton but an export efficiency that is high. Whereas in both manipulation experiments that is when the Fe quota for phytoplankton is lowered and when the zooplankton Fe stoichiometry is increased, there is a substantial increase in primary production (Figure 3a) and a seasonal bloom that is instead dominated by large phytoplankton and zooplankton. However, instead of being exported, the additional carbon being fixed is transferred into high concentrations of DOC (Figure 3h) driving a low export efficiency. This is particularly true for the experiment that increases zooplankton Fe stoichiometry, which decreases their biomass (Figure 3f), and drives an excess in nutrients that are allocated to the dissolved organic pool (Figures 3h and 3i). Although the improved seasonal cycle did not substantially change carbon export, achieving realistic bloom timing and amplitude remains essential for confidence in model projections and for ensuring chl *a* reflects biomass rather than photophysiological artifacts. The muted export response however highlights the complex links between seasonal production and carbon transfer to depth that may require further refinement and observational constraints to better resolve export variability.

4. Summary and Conclusion

This study showed that adjusting parameters associated with SO plankton traits, specifically, decreasing the phytoplankton Fe quota and increasing the zooplankton Fe stoichiometry, improves the model representation of the bloom seasonal cycle. It brings both the amplitude and timing of the bloom in the SAZ in line with satellite chlorophyll observations and couples the seasonal cycle of chlorophyll with phytoplankton carbon biomass. Despite the large increase in the amount of carbon being fixed in surface waters (and an increase in the dominant size structure of the community), there is no significant impact to the seasonal cycle of carbon export at 100 m. Instead, the higher productivity is tightly coupled with larger zooplankton and the majority of additional carbon being fixed in surface waters is recycled into DOC driving a low export efficiency (Henson et al., 2019; Le Moigne et al., 2016; Maiti et al., 2013). In conclusion, we demonstrate that improving the model representation of phytoplankton characteristics unique to the SO has a significant effect on enhancing the accuracy of the seasonal cycle in surface waters but has little impact on the amount of carbon exported to depth.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The model data used in this study is available at <https://doi.org/10.5281/zenodo.17067567> (Mashifane et al., 2025).

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