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Biogeochemistry of climate driven shifts in Southern Ocean primary producers

Ben J. Fisher[1], Alex J. Poulton[2], Michael P. Meredith[3], Kimberlee Baldry[4], Oscar Schofield[5], Sian F. Henley[1].

[1] School of GeoSciences, University of Edinburgh, Edinburgh, United Kingdom
[2] The Lyell Centre for Earth and Marine Science, Heriot-Watt University, Edinburgh, United Kingdom
[3] British Antarctic Survey, Cambridge, United Kingdom
[4] Institute for Marine and Antarctic Studies, College of Sciences and Engineering, University of Tasmania, Hobart, TAS, Australia
[5] Center of Ocean Observing Leadership, School of Environmental and Biological Sciences, Rutgers University, New Brunswick, NJ 08901, USA

Correspondence to: Ben J. Fisher (ben.fisher@ed.ac.uk)

Abstract. As a net source of nutrients fuelling global primary production, changes in Southern Ocean productivity are expected to influence biological carbon storage across the global ocean. Following a high emissions, low mitigation pathway, primary productivity in the Southern Ocean is predicted to increase by up to 40% over the 21st century. The ecophysiological response of marine phytoplankton experiencing climate change will be a key determinant in understanding the impact of Southern Ocean productivity shifts on the carbon cycle. Yet, phytoplankton ecophysiology is poorly represented in CMIP6 climate models, leading to substantial uncertainty in the representation of their role in carbon sequestration. Here we synthesise the existing spatial and temporal projections of Southern Ocean productivity from CMIP6 models, separated by phytoplankton class and identify key processes where greater observational data coverage can help to improve future model performance. We find bidirectional changes in iron and light limitation of phytoplankton, while the greatest changes in productivity occur in the coastal zone of the Southern Ocean. Different phytoplankton groups are responsible for driving productivity increases at different latitudes, yet we observe that models disagree on the ecological mechanism behind these productivity changes. We propose that an evidence-based sampling approach targeting climate-driven changes in ocean biogeochemistry and community assemblages in the regions of rapid projected productivity changes could help to resolve the empirical principles underlying phytoplankton community structure in the Southern Ocean.

1. Vulnerability of Southern Ocean ecosystems to climate change

The biological uptake of carbon by marine phytoplankton represents an increasingly important process in the Earth system, with ocean carbon storage mediating atmospheric CO_2 concentrations, including CO_2 of anthropogenic origin (Riebesell et al., 2007, Friedlingstein et al., 2022). The Southern Ocean is a disproportionately large carbon and heat sink relative to its size (Frölicher et al., 2015). Across the global ocean, uptake of carbon accounts for ~25% of CO_2 released by human activities

(Friedlingstein et al., 2022), with the Southern Ocean accounting for 30-40% of this global anthropogenic CO_2 uptake (e.g. Caldeira and Duffy, 2000, DeVries, 2014), predominantly due to enhanced atmosphere-ocean exchange at increased atmospheric CO_2 concentrations (Friedlingstein et al., 2022). While biological uptake is considered to play a minor role in total CO_2 uptake (Landschützer et al., 2015, Gruber et al., 2019), variability in pCO_2 has been associated with summertime blooms in the Southern Ocean (Gregor et al., 2018). Under a future climate scenario with longer growth seasons (Moreau et al., 2015), increased seasonal productivity (Leung et al., 2015, Fu et al., 2016) and a higher Revelle factor (Hauck et al., 2015), pelagic ecosystems are expected to become increasingly important in Southern Ocean carbon uptake (Henley et al., 2020).

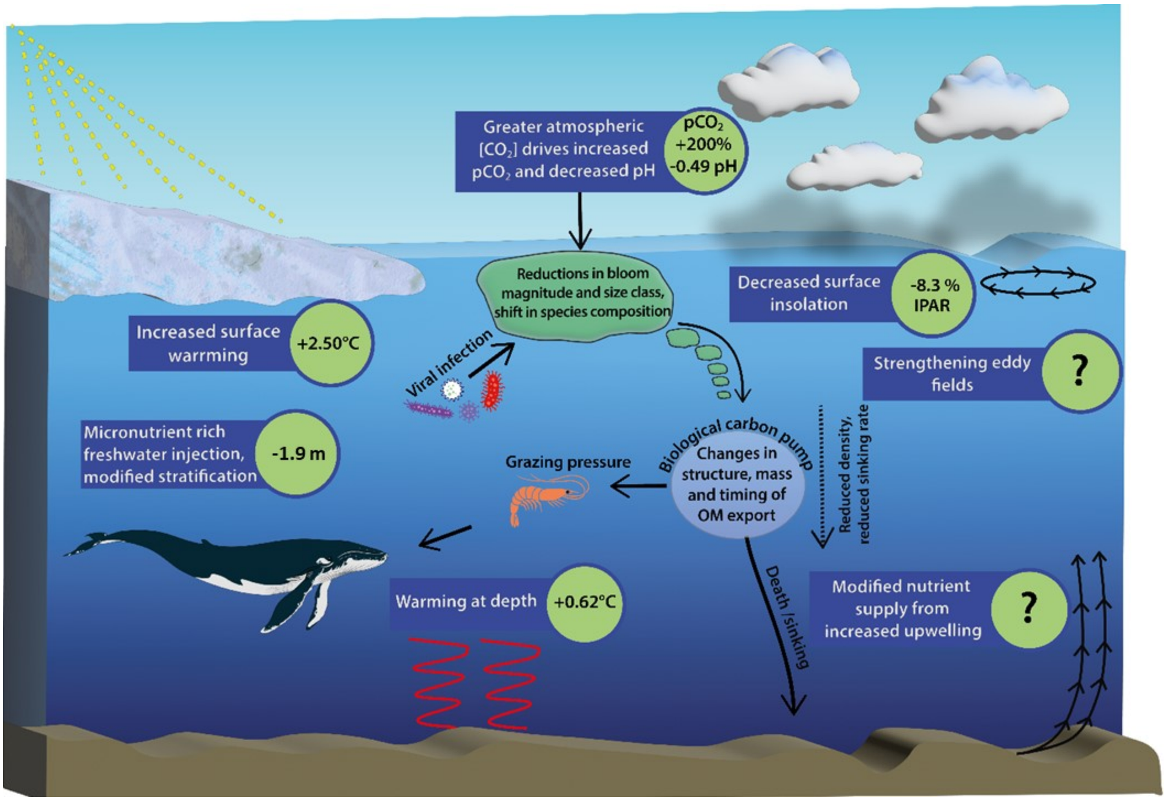

Figure 1: Schematic diagram of Southern Ocean pressures associated with climate change and the downstream biogeochemical consequences for ecosystem productivity. Values shown are 100 year mean changes to 2100 under a SSP5-8.5 scenario south of 65° and are taken from CMIP6 models and existing literature (see Table S2 for a full description). Question marks indicate processes where estimations of change do not exist.

Biological carbon cycling is especially vulnerable to climate change because of the small cell size of marine phytoplankton (0.002-0.2 mm), coupled with their specific requirements for light and iron, which are the preliminary factors limiting their growth in high nutrient low chlorophyll (HNLC) zones of the Southern Ocean (Moore et al., 2013). Primary production by Southern Ocean phytoplankton represents ~25% of global marine primary production, equivalent to 11.4 Pg C yr-1 (Okin et al., 2011). Climate impacts on Southern Ocean phytoplankton are likely to manifest in increased productivity (Leung et al., 2015, Fu et al., 2016), ecological shifts towards smaller cell sizes (Venables et al., 2013, Saba et al., 2014, Schofield et al., 2018, Mascioni et al., 2019, Biggs et al., 2019) and changes in seasonal phenology (Moreau et al., 2015). Increases in overall

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productivity can be most closely associated with reduced sea ice duration, increasing ocean surface area and light supply to the light and iron co-limited productivity system. Strengthened upwelling is also likely to increase sedimentary iron supply to the surface, however, the extent to which changes in ocean mixing can be expected to impact nutrient supplies remains largely unknown (Figure 1).

Shifts in community composition from diatoms to smaller cryptophytes have already been documented along the west Antarctic Peninsula (Montes-Hugo et al., 2008, Moline et al., 2008, Ducklow et al., 2007, Rozema et al., 2017, Moline et al., 2004), and are thought to be due to tolerance of cryptophytes to low-salinity waters induced by increased sea ice melt (Moline et al., 2004). Meanwhile, in culture-based competition experiments, diatoms are more successful in simulated future ocean conditions over prevalent haptophytes such as Phaeocystis antarctica, albeit with reduced diatom cell sizes (Xu et al., 2014). This difference is potentially driven by reduced iron limitation of diatoms and their greater tolerance to temperature change (Zhu et al., 2016). These varied responses between manipulation experiments and in situ observations suggest that physiological as well as ecological changes are important in understanding the net biogeochemical implications of phytoplankton community change.

In the sea-ice zone, grazing by zooplankton accounts for ~90% of phytoplankton losses (Moreau et al., 2020). Shifts in phytoplankton size class could rapidly cascade through the ecosystem as the dominant Southern Ocean zooplankton, krill are unable to graze the small cryptophytes (Haberman et al., 2003), instead promoting the dominance of carbon-poor salps (Salpa thompsoni), which reduces the overall efficiency of the marine food web (Ballerini et al., 2014) and potentially weakens the biological carbon pump (Biggs et al., 2021, Quéguiner, 2013). Additionally, water temperature, alongside changes to zooplankton abundance and diversity, has been shown to drive zooplankton metabolism (Mayzaud and Pakhomov, 2014), which can in turn be expected to modulate the grazing pressure and therefore the amount of POC exported. The Southern Ocean supplies 62 ± 5% of pycnocline nitrate and phosphate (Fripiat et al., 2021), therefore increased Southern Ocean productivity and regional nutrient utilization can be expected to reduce global nutrient export (Moore et al., 2018). Models of the Southern Ocean with complete nutrient trapping (no nutrient export) or no productivity (all nutrients available for export) suggest that regional nutrient supplies fuel 17 to 75% of productivity outside the Southern Ocean (Hauck et al., 2018, Primeau et al., 2013, Palter et al., 2010, Sarmiento et al., 2004).

Projections of productivity in the Southern Ocean under future climate scenarios from the Coupled Model Intercomparison Project Phase 6 (CMIP6) class Earth System Models (ESMs) are actively informing research directions, carbon budgets (Friedlingstein et al., 2022) and governmental policy (Touzé-Peiffer et al., 2020). Yet, between CMIP5 and CMIP6 the spread of model projections has increased as different models incorporate more complexity and additional processes (e.g. varying elemental stoichiometry, phytoplankton class diversity, complex elemental cycling) (Seferian et al., 2020). While representation of ocean physical drivers and nutrient fields compared to observations has improved between CMIP5 and

CMIP6, surface chlorophyll is one of three key parameters which did not show improvement in CMIP6 (Canadell et al., 2021, Fu et al., 2022). Deficiencies in model projections of phytoplankton and ocean biogeochemistry have been linked to the use of fixed C:N:P elemental stoichiometry (Kwiatkowski et al., 2018), and an inability to reflect physiological adaptations, e.g. the ability of diatoms to maintain growth under iron limitation (Person et al., 2018).

As the main source of organic carbon in the Southern Ocean, uncertainty in projections of phytoplankton composition compounds existing model uncertainty in the biological carbon flux to the ocean's interior and seafloor (Henson et al., 2022), where a fraction is available for long term storage. Simulations of phytoplankton productivity exert a particular bias on the Southern Ocean due to data scarcity resulting from weather conditions which impede chlorophyll remote sensing and sea ice preventing observation or sampling throughout the winter and early spring (Holm-Hansen et al., 2004, Laufkötter et al., 2018). Therefore, we argue that a targeted approach to establish phytoplankton-environment response interactions within the regions of the most rapid projected changes is essential to accelerate the improvement of phytoplankton representation in future generations of ESMs.

2. Physical climate driven changes in Southern Ocean water masses

Climate change is driving substantial changes in Southern Ocean water masses (Bindoff et al., 2019). The strengthening of Southern Ocean winds (Figure 2a) and increased buoyancy fluxes (including freshwater inputs) act as opposing drivers of stratification, modifying mixed layer depth (Figure 2b) and influencing iron and light availability to the upper ocean, thereby determining the abundance and composition of primary producers. Despite the importance of changes in Southern Ocean circulation for global ocean nutrient supply, the cumulative influence of microscale physical processes results in poor overall performance of CMIP-class models in this region when their historical runs are compared with observations (Meredith et al., 2019).

Across the Southern Ocean, the timing of the springtime onset of net primary production and the magnitude of summer biomass accumulation are controlled by light availability, as dictated by sea ice extent, cloud cover and water column structure (Henley et al., 2017). CMIP6 models project the greatest increase in productivity to occur across the coastal zone of the Southern Ocean (65-90°S) (Figure 2c), where irradiance limitation is reduced (Figure 2d) due to a shallowing of the mixed layer (Figure 2b) and increased light delivery in the Weddell Sea (Figure 2e), before experiencing stronger iron limitation (Figure 2f). Conversely, across the Transitional zone (40-50°S) the mixed layer deepens, incedental photosynthetically active radiation (IPAR) reduces, irradiance limitation increases and productivity increases are restricted compared to the rest of the Southern Ocean. Increased iron limitation (Figure 2f) likely manifests from greater competition for iron driven by increased productivity (Figure 2c) and a deepening of the mixed layer in the Subantarctic (50-65°S) (Figure 2b). Iron supply to the surface is subject to changes to the forcing and properties of water masses, resulting in variable circulation strengths, depth boundaries, heat content and carbon sequestration resulting from climate-driven perturbations to the ice-ocean-atmosphere system (Meredith et al., 2019, Bindoff et al., 2019). Upwelling of nutrients and light availability for phytoplankton are both strongly influenced by mixed layer depth, which in turn varies seasonally with increased solar warming and ice melt driving deeper Southern Ocean pycnocline stratification through the summer (Sallée et al., 2021).

Additionally, a substantial proportion of the extra energy resulting from zonal wind strengthening (Figure 2d) is imparted to the mesoscale eddy field (Meredith and Hogg, 2006, Hogg and Munday, 2014, Hogg et al., 2015). This intensification of the eddies may lead to regional enhancements in vertical mixing and nutrient supply, especially where it is co-located with regions of rugged bathymetry (Sheen et al., 2014) and sedimentary sources of iron (Ellwood et al., 2020, Uchida et al., 2020, Kahru et al., 2007). Increased near-surface wind strength has also been linked to reduced upper-ocean stratification and deeper mixed layers around the Southern Ocean (Carranza and Gille, 2015, Sallée et al., 2021), as models predict south of 55° (Figure 2b). However this is counteracted near to the coast by the stabilising influences of buoyancy forcing (Shi et al., 2020). Alongside wind strength, buoyancy forcing determines the strength of the meridional overturning circulation, responsible for atmosphere-ocean exchange of heat and carbon (Pellichero et al., 2018). Wind activity can drive increased outgassing of CO_2 from upwelling of deep waters (Mikaloff Fletcher et al., 2007, Lovenduski et al., 2008), resulting in a weakening of the Southern Ocean CO_2 sink (Le Quéré et al., 2007) and atmospheric CO_2 increases of up to 20 µatm (Lauderdale et al., 2013). This outgassing can be expected to increase with more intense storm events (Nicholson et al., 2022) and in line with sea ice retreat leaving a greater amount of ocean surface available for gas exchange (Shadwick et al., 2021).

Despite the importance of buoyancy in influencing atmosphere-ocean exchange, the sea ice changes that drive buoyancy forcing are poorly reproduced in CMIP6 models (Roach et al., 2020, Shu et al., 2020). Currently, CMIP6 models project a decrease in sea ice extent during the course of this century as warming continues, albeit with further work required to reduce uncertainties surrounding the magnitudes and timings (Roach et al., 2020). Stronger westerly winds enhance the northward export of sea ice in the Southern Ocean, promoting freshwater injection at more northerly latitudes, and enhancing stratification (Haumann et al., 2016), which will increase light availability. This northward flux also increases salinity at high latitudes (Pellichero et al., 2018), but this is compensated and exceeded regionally by increased discharge of glacial meltwater from the Antarctic Ice Sheet (Fogwill et al., 2015). This glacial discharge is likely to accelerate under continued warming in both West and East Antarctica, with the Amundsen and Bellingshausen Seas likely to be impacted most rapidly, and accelerating freshwater discharge reaching as far west as the Ross Sea (Levermann et al., 2014, Meredith et al., 2019). Recent large and unexpected changes in sea ice around Antarctica emphasise that greater knowledge of the key drivers and controls is required, in order to improve predictive skill in models (Turner and Comiso, 2017).

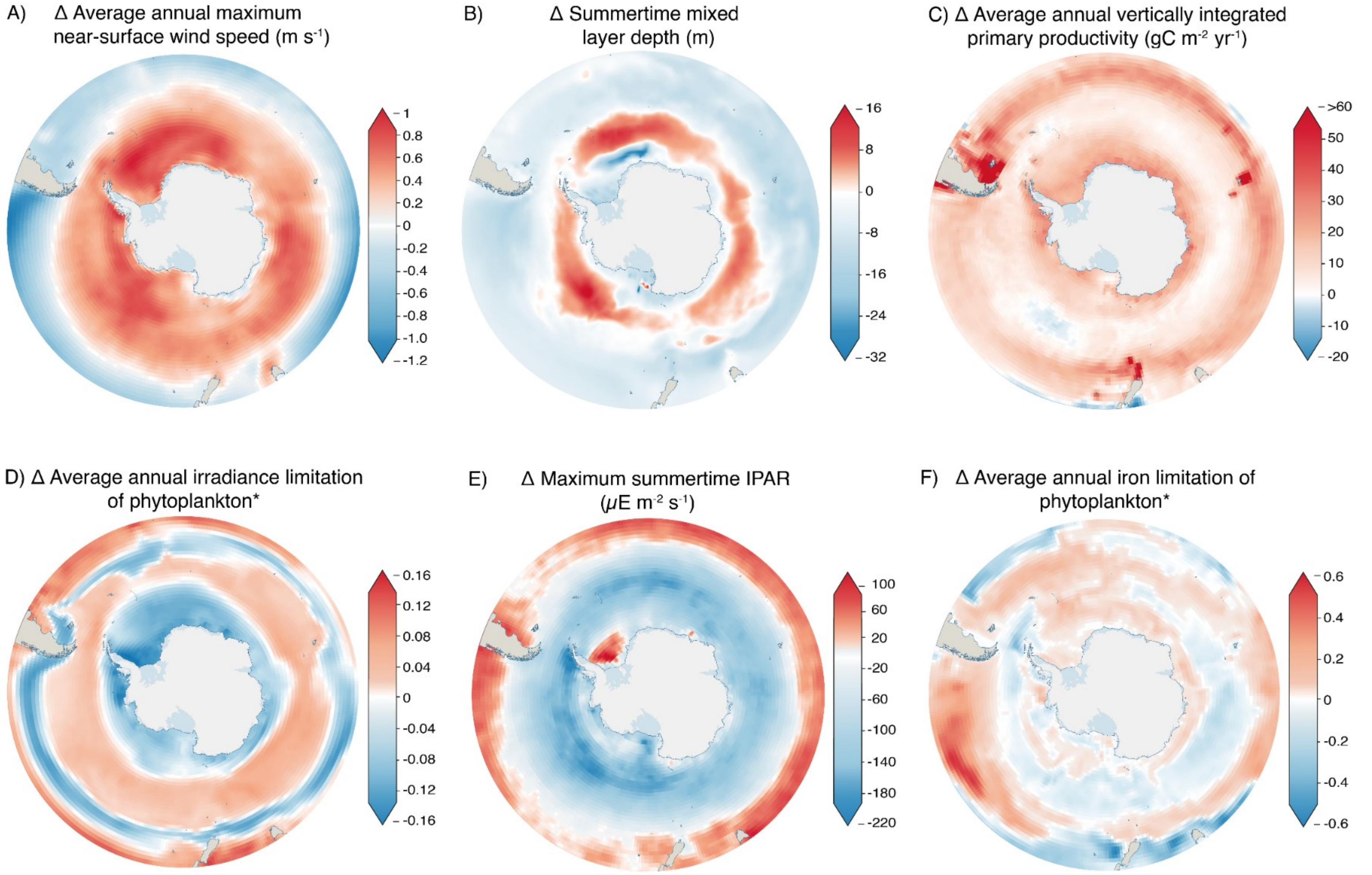

Figure 2: CMIP6 anomaly representing 100 year change in A) near-surface wind speed, B) mixed layer depth, C) primary productivity, D) irradiance limitation of phytoplankton, E) incedental photosynthetically active radiation (IPAR),F) iron limitation of phytoplankton. Changes are calculated from an ensemble of CMIP6 models, comparing a historical (1985-2015) average against 2100 under the SSP5-8.5 climate scenario. Details of ensemble members are given in Table S1. *Units in panels E and F are arbitrary ratios of growth under environmental irradiance or iron concentrations against potential growth under unlimited irradiance or iron concentrations.

3 Changing biogeochemistry of the Southern Ocean

3.1 Micronutrient supply and uptake

Iron acts as the primary limiting nutrient across the Southern Ocean (Watson et al., 2000, de Baar et al., 1995), due to supply limitation from low atmospheric inputs and distance from terrigenous sources (Boyd and Ellwood, 2010). Around the Antarctic coast, iron concentrations are set by processes including the resuspension of shelf sediments (Blain et al., 2001), melting of sea ice (Lannuzel et al., 2016) and potential transformation of iron into more labile forms by glacial retreat, as seen in the Arctic (Laufer-Meiser et al., 2021). While supplies of ice-rafted iron in the open ocean (Hopwood et al., 2019, Raiswell et al., 2008) may be expected to increase with warming, this increase in supply appears to be offset by an increased total iron demand to support enhanced phytoplankton growth, stimulated by increased light availability (Figure 2a). Much of the Southern Ocean relies on regenerated iron (i.e. that released from remineralisation), denoted by the fe ratio (uptake of new iron divided by uptake of new and recycled iron), with a value of ~0.1 in HNLC waters beyond the coastal zone (Bowie et al., 2009, Boyd et al., 2005). Therefore, the class of phytoplankton present in any region will act as a determinant on iron resupply since physiological differences between phytoplankton species will influence sinking rate, cellular iron content, and the rate of remineralisation. While iron is known to be an essential micronutrient for phytoplankton, there are large uncertainties in our understanding of iron cycling, particularly in parameterising rates of ligand adsorption and desorption (Tagliabue et al., 2016). Shifts in primary producers may influence rates of iron ligand sorption and desorption by to modulating the size and molecular composition of the organic ligand binding pool.

Iron is utilised by phytoplankton in key metabolic processes, including the production of electron transfer proteins used within photosystems, for the reduction of carbon dioxide, sulphate and nitrate, and synthesis of chlorophyll (Street and Paytan, 2005). Other micronutrients beyond iron, predominantly manganese, have been shown to play an important role in controlling oxidative stress by catalysing antioxidant production in some diatom species (McCain et al., 2021), explaining the observed phenomena of iron-manganese co-limitation in the Southern Ocean (Browning et al., 2021, Pausch et al., 2019, Balaguer et al., 2022). Despite the importance of micronutrients such as manganese in controlling phytoplankton growth, particularly during seasonal transitions (Browning et al., 2021), only iron is considered in ESMs, due at least partially to the lack of observational data to underpin distribution modelling of other micronutrients. Future work should continue to develop our understanding of the metabolic role of other micronutrients and additionally consider the extent to which diversity exists in micronutrient demand between Southern Ocean phytoplankton species.

3.2 Macronutrient supply and uptake

Nitrogen species, silicic acid (DSi) and phosphate are essential for the growth and survival of diatoms, with nitrate and phosphate also being required by all other phytoplankton classes for cellular metabolism. The ratio of utilisation between nitrogen (N) and phosphorus (P) deviates from the Redfield (1958) ratio of 16:1 across the Southern Ocean according to changes in community composition (Henley et al., 2020, Weber and Deutsch, 2010). Unlike much of the global ocean (Moore et al., 2013), high rates of macronutrient supply from the Circumpolar Deep Water (CDW) prevent widespread N or P limitation in the Southern Ocean except in periods of intense summer growth in high-productivity coastal regions (Henley et al., 2017). Although projections indicate an increase in biomass across such regions (Figure 3), models do not show any increases in nitrate limitation over the remainder of the century, suggesting that iron and light will continue to be the primary constraints on productivity.

While macronutrients are not usually limiting to Southern Ocean phytoplankton, growth of diatom communities, particularly around high productivity coastal and island zones (supported by lateral iron advection) (Robinson et al., 2016), is likely to place an increased demand on DSi availability (Table 1). The relationship between Si and N is denoted as Si* ([Si(OH)4]–[NO3–]) (Sarmiento et al., 2004), with high Si* values (> 25) indicating plentiful DSi availability that supports diatom growth, while low values (< 10) suggest conditions which favour non-silicifying phytoplankton, such as the smaller cryptophytes and haptophytes. Si* is highest in the Antarctic zone (Henley et al., 2020) because of silica input from upwelling of CDW, but remains spatially heterogeneous within this region (Table 1). Si* is consistently high in the Weddell Sea, while across the WAP and Ross, Amundsen and Bellingshausen Seas there is a moderate mean Si* with large variability, and the Indian Sector has a substantially lower DSi availability. The relative availability of DSi is generally reflected in projected patterns of chlorophyll over the current century; large increases in chlorophyll are projected in the Weddell Sea with much less growth in the Indian sector (Figure 3), suggesting that Si limitation of diatoms will continue to constrain overall patterns of phytoplankton productivity.

The impact of climate change on DSi supply to the surface is difficult to evaluate because it is dependent on the competing stratification effects from strengthening upwelling and an increase in freshening. Export of DSi from the surface and remineralisation at depth additionally act as important controls on supply; more rapid remineralisation of organic matter in the upper ocean as warming increases the microbial respiration rate may increase demand for OM and release nutrients at shallower depths. Such an effect would also reduce both the rain rate and the quality of OM available at the seafloor for long-term carbon sequestration. Increases in viral lysis under warmer ocean conditions will also influence nutrient dynamics either by retaining nutrients at the surface through shallow cell lysis and remineralisation (Biggs et al., 2021), or by shuttling nutrients to depth when infection of iron-limited cells delays death and increases sinking (Kranzler et al., 2021). Efforts to better define the nutrient budgets, particularly in low sea ice years, across different sectors of the Southern Ocean, as well as understanding the

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changing nutrient demands of phytoplankton will be essential for determining future trends in nutrient limitation (Henley et al., 2019).

3.3 Ocean acidification

Across all regions of the Southern Ocean, continued uptake of anthropogenic CO_2 is expected to elicit a decrease in pH of ~0.45 units south of 55°S (Table 1). While ocean acidification (OA) is typically considered to have the greatest effect on marine calcifiers through impacts on the production and dissolution of calcium carbonate (Figuerola et al., 2021), OA is also likely to impact diatom (Petrou et al., 2019), picophytoplankton (Tortell et al., 2008) and krill (Kawaguchi et al., 2013) populations which form the base of Southern Ocean ecosystems. Unravelling the specific impact of OA on phytoplankton species is complex due to the fact that OA often acts on phytoplankton indirectly, for example Petrou et al. (2019) showed that acidification reduces silicification of diatoms, likely reducing sinking capacity and increasing rates of remineralisation in the upper ocean, in turn weakening ocean carbon drawdown and acting as a positive feedback on the carbon cycle. Additionally, in their experiment, Petrou et al. (2019)'s modelled OA conditions resulted in reduced photosynthetic capability showing a direct effect of OA on diatom physiology. OA has further been shown to elicit change in biogeochemical parameters such as carbon uptake, with reduced carbon uptake by Ross Sea assemblages under elevated pCO_2 concentrations (Tortell et al., 2008). However, this effect may be offset or reversed by overall increases in productivity linked to shifts towards larger diatom species under increasing OA (Tortell et al., 2008). Alternativley, some studies have shown that smaller size classes (<20 µm) are more successful at higher pCO_2 values (Hancock et al., 2018) or that total productivity may decrease under OA (Westwood et al., 2018).

The ability for OA to promote increased productivity has been linked to the availability of Fe and species shift effects (Hoppe et al., 2013), whereby species with the greatest capacity to tolerate variability in pH (e.g. Fragilariopsis cylindrus, Chaetoceros sp.) outcompete less tolerant, typically faster growing species such as Pseudo-nitzschia (Hoppe et al., 2013, Tortell et al., 2008). At an ecosystem level, OA has been shown to reduce the lipid content, and therefore nutritional value of large phytoplankton to zooplankton grazers (Duncan et al., 2022). While protein and lipid content of small taxa may increase, their poor utilisation due to size will likely lead to rapid remineralisation in the surface layer, further reducing energy transfer to higher trophic levels. The impacts of OA on phytoplankton ecology and physiology are not currently reflected in CMIP6-class ESMs (Seferian et al., 2020), but are likely to become increasingly important in the future as the rate of OA increases. To support this development, empirical research will need to focus on further disentangling the indirect influences of OA on phytoplankton on a species-specific basis, particularly for picophytoplankton which are less well studied in incubation experiments but are expected to become more abundant. The interspecies divergence of responses to OA, and differential responses at different pCO_2 thresholds suggests that OA-induced ecophysiological change is likely to remain too complex to model accurately at the basin or global scale.

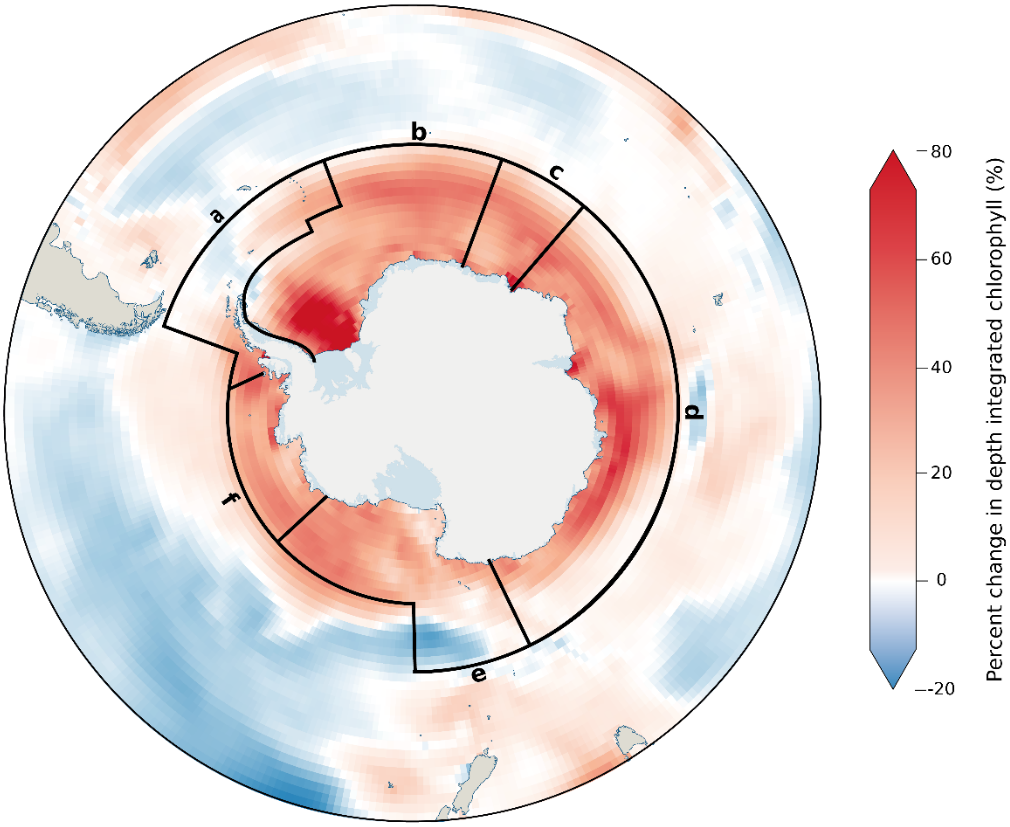

Figure 3: Change in depth-integrated chlorophyll (0-500 m) from all phytoplankton, displayed as the percentage change between the annual historical average (1985-2015) and projected values for 2100. Values shown are multi-model means of the models listed in Table S1. Spatial boundaries show the Southern Ocean Observing System (SOOS) regions south of 55°S, which are defined in Table 1.

Table 1: Biogeochemical parameters of the Southern Ocean Observing System regions. SOOS regional working groups (as defined at: www.soos.aq/activities/rwg) indicated on Figure 3; section C is an overlap section of sections B and D. Data shown are: Si* ($[Si(OH)_4]-[NO_3^-]$) values determined from World Ocean Atlas 2018 data, multi-model means of pH and temperature anomalies based on comparisons between the mean annual historical value (1985-2015) and projected values for 2100 under SSP5-8.5 for a CMIP6 ensemble (detailed in Table S1). Values in brackets are standard deviations.

Section	**SOOS Region**	**Si***	**Δ pH**	**Δ Temperature (°C)**
A	West Antarctic Peninsula & Scotia Arc	**17.24 (17.82)**	**-0.45 (0.01)**	**1.99 (0.40)**
B	Weddell Sea & Dronning Maud Land (WSDML)	**37.37 (9.70)**	**-0.43 (0.01)**	**1.61 (0.49)**

C	SOIS/WSDML	**23.16** **(6.67)**	**-0.44** **(0.01)**	**2.09** **(0.37)**
D	Southern Ocean Indian Sector (SOIS)	**4.71** **(3.72)**	**-0.44** **(0.01)**	**1.99** **(0.52)**
E	Ross Sea	**19.82** **(18.49)**	**-0.42** **(0.02)**	**1.16** **(0.47)**
F	Amundsen and Bellingshausen Seas	**17.59** **(14.02)**	**-0.45** **(0.01)**	**1.97** **(0.32)**

4 Primary production and representation in CMIP6

4.1 Productivity parameters

Across CMIP6 models, primary productivity is expressed as the depth-integrated production of particulate organic carbon (POC, as intpp) and the biomass of phytoplankton expressed as chlorophyll (Chl). While chlorophyll and POC production both represent phytoplankton related parameters, they are independent variables, with the relationship between the two (Chl/C ratio) being spatially and seasonally variable across the Southern Ocean (Thomalla et al., 2017). Additionally, the biological origin of POC in CMIP6 differs based on the ecosystem complexity of different models, for example between those models which include bacteria and those which do not (Table 1 in Seferian et al. (2020)). Although Chl/C ratios are fundamental in coupling marine ecosystems to the biological carbon pump, estimates of Chl:C carry substantial uncertainties, particularly when sensed remotely (Baldry et al., 2020). Resolving these uncertainties, stemming from non-photochemical quenching, interference from non-phytoplankton POC, and differences in intracellular chlorophyll contents between phytoplankton species (Baldry et al., 2020) will improve our ability to utilise satellite- and Argo-derived ocean chlorophyll data and improve ecosystem-carbon coupling across ocean biogeochemical models.

4.2 Phytoplankton classes

A major difference in the representation of productivity between CMIP6 models is the extent to which they consider different classes of phytoplankton. Diatoms (>20 µm) and pico/nano phytoplankton (predominantly cryptophytes and haptophytes) represent the vast majority of productivity across all latitudes of the Southern Ocean. Diatoms are a significant contributor to primary production and carbon export, accounting for ~40% of global marine primary production and POC exported to depth in the ocean (Treguer and De La Rocha, 2013, Jin et al., 2006). Diazotrophs (nitrogen-fixing phytoplankton) are present in small numbers, usually only in environmental niches, due to the excess supply of nitrogen across the Southern Ocean (Nissen et al., 2018). Calcifiers, mostly coccolithophores, inhabit waters north of 60°S where there is a strong supply of light but low Si, high Fe conditions, preventing the growth of diatoms (Charalampopoulou et al., 2016). Of ~90 distinct models (excluding multiple resolutions of the same model) included in CMIP6, 11 specifically include diatoms under future warming conditions and only three of these additionally consider picophytoplankton. Two CMIP6 models (GFDL-ESM4 and CESM2-WACCM) showed substantial differences in productivity projections south of 65° (Figure 3). While GFDL-ESM4 projects that in this region diatoms account for the majority (55%) of the change in productivity under SSP5-8.5 (Figure 4a,b), diatoms represent only 26% of productivity in CESM2-WACCM, while picophytoplankton form the major (74%) phytoplankton group (Figure 4e,d). Additionally, the GFDL model indicates that increased productivity is driven by increases in both diatoms and picophytoplankton, representing a simultaneous growth scenario while CESM2-WACCM favours a replacement mechanism with diatoms decreasing as picophytoplankton populations grow (Figure 4c,f. This demonstrates that further parameterisation is itself not a solution to integrating phytoplankton ecophysiology while fundamental gaps remain in the empirical understanding of mutualism and resource limitation between phytoplankton classes. Here, we argue for an expansion in the biological understanding of phytoplankton responses to climate, moving beyond single species to community based experiments alongside a shift towards holistic marine ecosystem models which account for an expanded range of biological interactions including phytoplankton-zooplankton predation and bacterially-driven mixotrophic effects (Seferian et al., 2020). Trait-based approaches have been explored as a means of modelling phytoplankton community composition, distinguishing functional groups based on life histories, morphology and physiology (Litchman and Klausmeier, 2008). Ocean biological sampling has some of the lowest coverage in the Southern Ocean (Sunagawa et al., 2020). The lack of coverage compounds uncertainty associate with the unique phytoplankton traits in the region, for example the lack of nitrogen fixation and cryobiological traits such as ice-binding, resulting in a weak overall understanding of Southern Ocean phytoplankton biology. Expansion of ecosystem observing at the metagenomics level offers a promising opportunity to expand our knowledge of traits and trade-offs in Southern Ocean phytoplankton communities, facilitating their integration into ocean climate models.

4.3 Ecological dynamics and ecophysiology

In a changing ocean, phytoplankton will succeed where they have the greatest biological plasticity, for example the ability to photo-acclimate rapidly (Arrigo et al., 2010) or scavenge and utilise a diverse range of micronutrients. The physiological properties of any individual species ultimately determines their ability to survive in a particular region at a particular time under ever changing climate-driven conditions. Subsequently, species ecology determines the abundance and temporal extent with which a species can exist or compete in a particular region. As the warming of the climate continues to bring about an earlier retreat of sea ice, growth seasons are expected to lengthen, altering the temporal dynamics of species progression (Moreau et al., 2015). In the coastal zone of the Southern Ocean, changes in light appear to be the main influence on productivity with decreased irradiance limitation stimulating picophytoplankton growth to a greater extent than diatoms

(Figure 4 j,k,m,n); meanwhile iron limitation shows little correlation with productivity changes in this region (Figure 4 g,h), likely because of replete iron supplies from coastal upwelling.

While few CMIP6 models account for multiple phytoplankton groups, among the models that do contain different classes there is a vast variability between the magnitudes of change they project over the century (Figure 5). Accurate representation of the seasonal progression of phytoplankton in models is important because pre-bloom community composition is closely linked to the eventual extent of the summer bloom (Biggs et al., 2019). In addition, the magnitude of early spring and late autumn productivity is likely to constrain the length of the grazing season for zooplankton and food supply to benthic communities (Constable et al., 2014). Early season productivity is known to occur in under-ice algal communities (Lizotte, 2001), and potentially by phytoplankton (Ardyna et al., 2020), which makes both in situ and satellite measurements of this productivity even more complex due to the physical and reflective barrier of sea ice. Sensing early season under-ice productivity represents a strategic priority because of the likely effect of climate change in producing shifts in seasonal timing related to earlier sea ice retreat, potentially shifting the summer bloom timing or amplitude. The Intergovernmental Panel on Climate Change (IPCC) notes that lack of data relating to snow cover on Antarctic sea ice limits mass balance estimations, and therefore results in a “very limited predictive skill” for ice-dependent ecosystems (Meredith et al., 2019). Subsequently, expanded understanding of productivity onset and early season physiology and phenology will allow for better integration of phytoplankton ecophysiology in ESMs, which has been identified as a step change required to improve biogeochemical processes and climate projections in future generations of CMIP (Seferian et al., 2020).

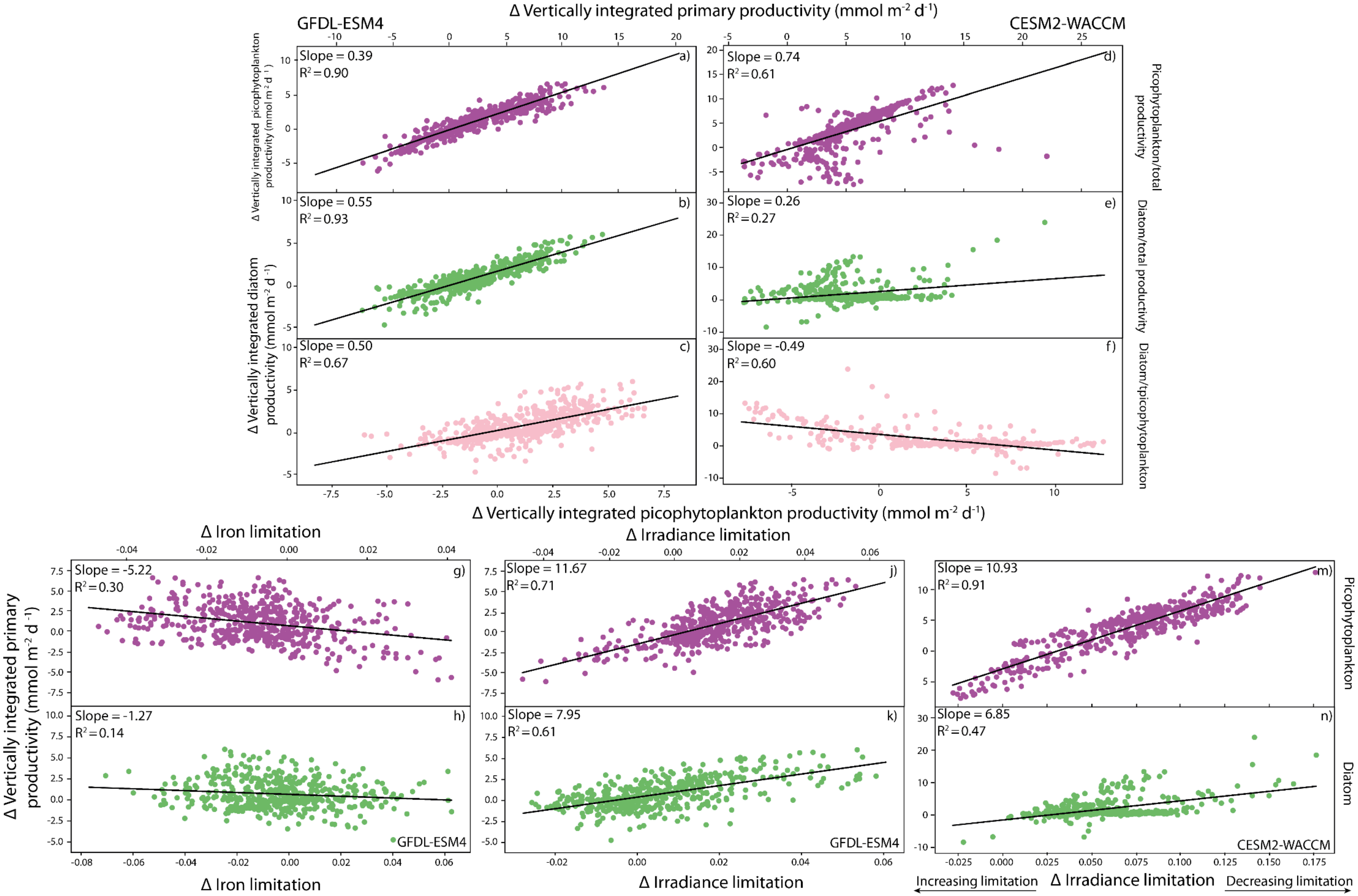

Figure 4: Evalution of GFDL-ESM4 and CESM2-WACCM models using an anomoly between 2100 (SSP5-8.5) and a historical average (1985-2015). Linear regression between change in total productivity and picophytoplankton productivity for GFDL-ESM4 (A) and CESM2-WACCM (D). Linear regression between change in total productivity and diatom productivity for GFDL-ESM4 (B) and CESM2-WACCM (E). Linear regression between change in picophytoplankton productivity and diatom productivity for GFDL-ESM4 (C) and CESM2-WACCM (F). Change in iron limitation with picophytoplankton (G) and diatom (H) productivity for GFDL-ESM4. Change in irradiance limitation with picophytoplankton (J) and diatom (K) productivity for GFDL-ESM4. Change in irradiance limitation with picophytoplankton (M) and diatom (N) productivity for CESM2-WACCM.

5. CMIP6 Projections

From those models that do distinguish between at least diatoms and other phytoplankton (Table S1) we are able to examine projected changes in community composition over the 21st century under a continued warming scenario (SSP5-8.5) (Figure 5). In CMIP5, Leung et al. (2015) found a latitudinally banded response of phytoplankton to continued warming, driven by the bottom-up dynamics of nitrate, iron and light limitation. From this, we applied the same latitudinal bands to our analysis of the changes in whole community, diatom and non-diatom productivity across CMIP6. Our whole community projections agree with the trends shown by Leung et al. (2015), showing a southward movement of phytoplankton productivity, increasing average total productivity south of 40°S, with the strongest increases in the Transitional (40-50°S; 14 g C m^{-2} yr^{-1}) and Antarctic (or coastal) zones (65-90°S; 16 g C m^{-2} yr^{-1}). In relative terms, this reflects a ~10% increase in total productivity over the SSP5-8.5 run (2015-2100) for both the Transitional and Subantarctic zones, with a ~40% increase in productivity for the Antarctic zone (Figure S4). An ensemble mean shows no overall change in productivity across the Subtropics, however individual models show the widest degree of divergence in this region, indicating a large amount of uncertainty in the directionality of productivity change.

In the Transitional zone, we initially see growth in the proportion of productivity linked to diatoms at a rate greater than that of non-diatoms until 2085, likely stimulated by increased iron availability (Figure 2f). Between 2085 and 2100, this trend is inverse with non-diatom productivity overtaking diatoms, potentially reflecting the increase in light limitation across the region (Figure 2d) which favours smaller, less light-dependent, phytoplankton. In the Subantarctic (50-65°S), despite a large projected increase in light availability (Figure 2e), models project only a minor increase in productivity driven by a small amount of diatom growth, suggesting that growth of both diatom and non-diatom species remains largely iron-limited in this region. The coastal zone shows the greatest degree of change in phytoplankton growth; by 2100 the non-diatom population will have increased at twice the rate of diatoms. The continued increase in all phytoplankton classes can be attributed to the increased iron availability (Figure 2f), with the success of non-diatoms reflecting the increase in light limitation (Figure 2e). While CMIP6 models do not explicitly consider phytoplankton size, the shift from diatoms to, typically smaller, non-diatom species is consistent with more advanced ecological models such as DARWIN which predict a decrease in the slope of the phytoplankton size spectrum, albeit over a greater area of the Southern Ocean than shown in CMIP6 (Henson et al., 2021). Despite the clear differences between latitudinal bands, spatial heterogeneity continues to exist within these zones, particularly for the coastal zone where the majority of change occurs on the WAP and Weddell Sea (Figure 3), reflecting the disproportionately high DSi supply in these regions (Table 1). Resolving spatial heterogeneity of phytoplankton in global-scale models such as those in CMIP6 is likely to require an increased reliance on, and integration with, regional-scale modelling (Person et al., 2018). The rapid increase of non-diatom species around the coast is in agreement with studies describing declining large diatom (>20 µm) abundances (Wright et al., 2010, Kang et al., 2001, Pearce et al., 2011); however, while it is true that diatoms are projected to decrease as a proportion of the community, diatom-derived carbon production is still projected to increase under continued warming, suggesting that the coastal biological carbon pump may be less threatened by this shift in community composition than previously thought.

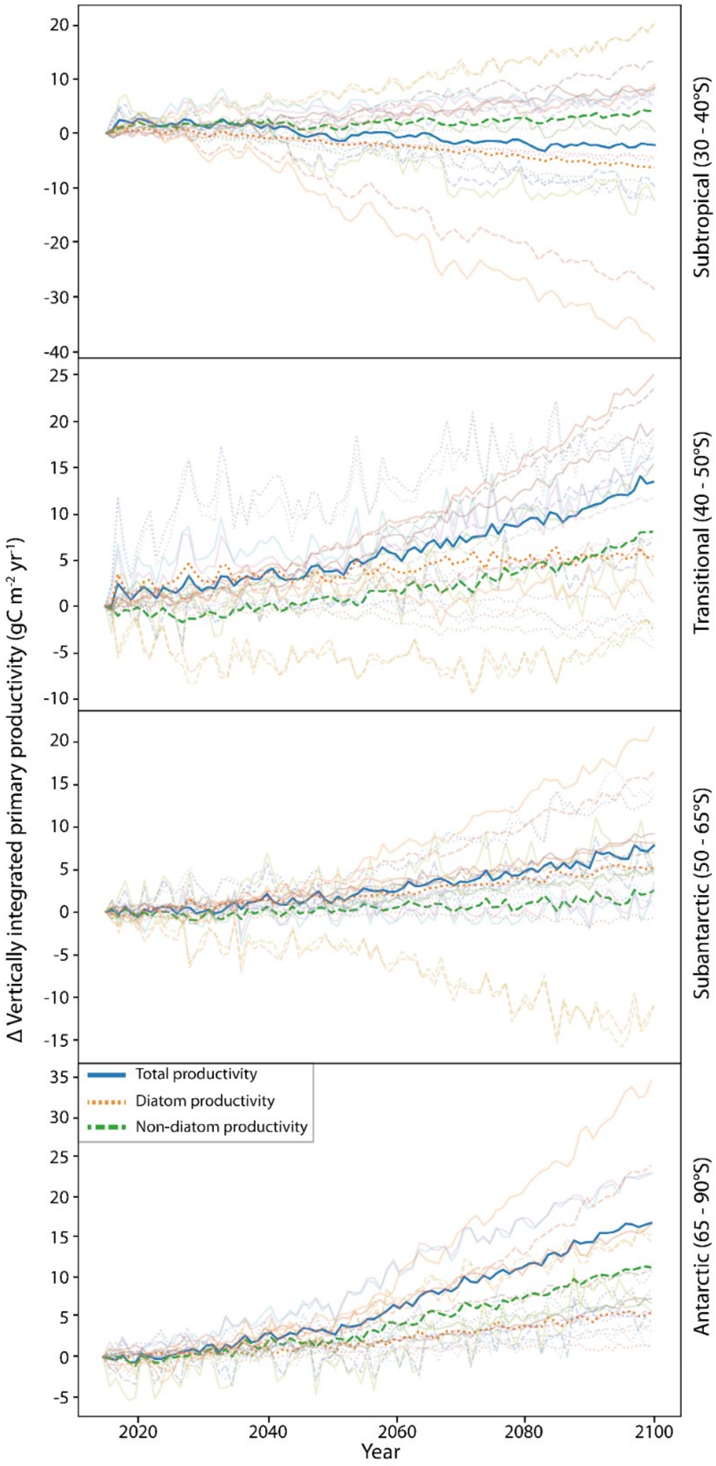

Figure 5: Changes in productivity (g C m^{-2} yr^{-1}) and the contribution of different phytoplankton classes to productivity, 2015-2100. The anomaly in CMIP6 model productivity projections (as POC production) compared to 2015 for SSP5-8.5 conditions across 4 latitudinal bands of the Southern Ocean, per Leung et al. (2015). Thick lines represent multi-model means of total productivity (intpp), diatom productivity (intppdiat) and non-diatom productivity (intpp-intppdiat). Light lines represent the individual model projections. Details of the models assessed are given in Table S1.

6. Global implications of Southern Ocean productivity shifts

The impact of climate change on phytoplankton has the potential to restructure ecosystems of the Southern Ocean, with wider consequences for global productivity and climate. Earth System Models are essential for understanding the impact of regional scale processes on global climate, and CMIP6 represents our best understanding of future climate change under continued warming. Despite this, key processes that will impact phytoplankton are absent from most models, resulting in large uncertainty for all phytoplankton classes across all zones of the Southern Ocean. While computational limits prevent ecological parameterisation on the scale of purely biological models, the lack of empirical understanding prevents inclusion of some key physical and biological processes in these models.

We have identified changes in nutrient upwelling (both upwelling strength and concentration of nutrients at the surface), directionality of mixed layer depth change, mutualism and resource competition between phytoplankton classes, and eddy strengthening as key processes which require improved representation in future generations of climate models. In some cases this is because of lack of monitoring (nutrients, eddies), while the relatively recent reversal in Antarctic sea ice trends means it is not yet possible to determine the scale of coastal MLD change from excess freshwater injection. Additionally, there is a need for ongoing monitoring of phytoplankton functional group composition, particularly in areas of the greatest projected change (WAP and Weddell Sea), ideally capturing temporally-resolved new productivity in the early spring. Crucially, to then link ecological shifts to global climate, the diversity in fate of phytoplankton species represents a substantial knowledge gap required for improving the predictive ability of ESMs. Finally, there is a need for process-based studies including a diverse set of phytoplankton species to further our understanding of fundamental life cycle processes and ecological-biogeochemical coupling. A focus towards defining variability in phytoplankton buoyancy, carbon uptake and release as DOM, grazing by zooplankton, interactions with viruses, macronutrient stoichiometry and micronutrient utilisation will enhance our core understanding of Southern Ocean phytoplankton dynamics in a changing climate.

7. Methods

Model and observational data for the Southern Ocean were collected and visualised to determine a) the physical and biogeochemical changes which force or result from shifts in productivity, b) the extent of primary productivity shifts in CMIP6.

7.1 CMIP projections

Model output was obtained from the Climate Model Intercomparison Project Phase 6 (CMIP6) data server via pangeo.io using the XMIP package in Python on JASMIN (Lawrence et al., 2013). Ensemble members for each parameter were chosen based on their availability for historical and SSP5-8.5 (ScenarioMIP) data (O'Neill et al., 2016). Some models that were available were not included in the analysis due to compatibility issues where significant differences in data structure existed. All variables were initially selected with monthly frequency except for surface winds where data were initially obtained daily; subsequently, annual means were generated for all parameters.

Model data were processed in python to apply the desired analysis (e.g. annual average, annual maximum) and then further averaged over residual variables (e.g. member_id). Subsequently, all models were re-gridded to a common grid using XESMF before being averaged to create multi model means.

For spatial plotting, data were exported from python and a common area of the grid selected in Climate Data Operator. The subset data were projected to the Antarctic Polar Stereographic (3031) coordinate reference system in ArcGIS pro. Finally, spatial plots were visualised in QGIS using the Quantarctica (Matsuoka et al., 2021) package, with post processing using SAGA and GDAL tools to remove imperfections in grid alignment through interpolation. The full range of CMIP6 parameters accessed, models evaluated and transformations applied are detailed in Table S1. All code to extract, analyse and visualise CMIP6 data is available open access.

7.2 Regional data

Si* across the Southern Ocean was mapped from the World Ocean Atlas 2018 data product (Garcia et al., 2019). Annually averaged data for nitrate and silicic acid were exported at a 1x1 degree resolution and subtracted from one another to produce Si*. The output was visualised in QGIS using Quantarctica base layers (Matsuoka et al., 2021). For Si*, pH and temperature values by SOOS area, SOOS regions south of 55° were drawn as mask layers and subset using the zonal statistics function in QGIS.

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Data availability

CMIP6 data were obtained through, and are freely available at panego.io. Specific models and parameters extracted for each analysis are listed in Supplementary Table 1. Code for CMIP6 data analysis are available at: *(zenodo link to be later inserted, available to reviewers as attached zip file)*.

Author contributions

BJF, SFH, MPM and AJP devised the concept for the paper and contributed towards initial drafting and editing. BJF performed model analysis and produced the figures. OS and KB provided input on conceptual design and edited previous versions of the manuscript.

Competing interests

The authors declare no competing interests.

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