Anthropogenic climate change drives non-stationary phytoplankton variance

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Abstract. Multiple studies conducted with Earth System Models suggest that anthropogenic climate change will influence marine phytoplankton over the coming century. Light limited regions are projected to become more productive and nutrient limited regions less productive. Anthropogenic climate change can influence not only the mean state, but also the variance around the mean state, yet little is known about how variance in marine phytoplankton will change with time. Here, we quantify the influence of anthropogenic climate change on internal variability in marine phytoplankton biomass from 1920 to 2100 using the Community Earth System Model 1 Large Ensemble (CESM1-LE). We find a significant decrease in the internal variance of global phytoplankton carbon biomass under a high emission (RCP8.5) scenario, with heterogeneous regional trends. Decreasing variance in biomass is most apparent in the subpolar North Atlantic and North Pacific. In these high-latitude regions, zooplankton grazing acts as a top-down control in reducing internal variance in phytoplankton biomass, with bottom-up controls (e.g., light, nutrients) having only a small effect on biomass variance. Grazing-driven declines in phytoplankton variance are also apparent in the biogeochemically critical regions of the Southern Ocean and the Equatorial Pacific. Our results suggest that climate mitigation and adaptation efforts that account for marine phytoplankton changes (e.g., fisheries) should also consider changes in phytoplankton and zooplankton variance driven by anthropogenic warming, particularly on regional scales.

1 Introduction

Anthropogenic climate change has significantly impacted marine ecosystems from phytoplankton (Bopp et al., 2001, 2013; Laufkötter et al., 2015; Kwiatkowski et al., 2020) to fish (Perry et al., 2005; Cheung et al., 2009, 2010; Mills et al., 2013; Wernberg et al., 2016; Flanagan et al., 2018; Staudinger et al., 2019). As the base of the marine food web, phytoplankton support diverse marine ecosystems by providing food for higher trophic levels (Falkowski, 2012). Constraining future changes in phytoplankton with anthropogenic warming is important at regional scales for fisheries adaptation (Pauly and Christensen, 1995; Chassot et al., 2010; Link and Marshak, 2019; Marshak and Link, 2021), particularly as phytoplankton biomass is incor-

porated into offline fisheries models to predict changing catch potential (Christensen and Walters, 2004; Travers-Trolet et al.,
2009; Lehodey et al., 2010; Maury, 2010; Blanchard et al., 2012; Christensen et al., 2015; Jennings and Collingridge, 2015;
Tittensor et al., 2018; Petrik et al., 2019; Heneghan et al., 2021). In this context, understanding changes in both phytoplankton

25   biomass and its variance is essential in reducing uncertainty in marine ecosystem projections.

The abundance and distribution of phytoplankton, the base of the marine food web, will likely change with anthropogenic
warming. Future projections of climate change impacts reveal a global loss of marine net primary production (NPP) and
phytoplankton biomass, particularly at middle and low latitudes (Steinacher et al., 2010; Bopp et al., 2013; Lotze et al., 2019;
Tittensor et al., 2021). A majority of Earth System Models (ESMs) project an increase in phytoplankton abundance in the high

30   latitude ocean as light limitation is alleviated by stratification, increasing temperature stimulates photosynthesis, and sea ice
cover declines. In contrast, a decrease in the low latitude oceans is projected as nutrient limitation from thermal stratification is
enhanced (Steinacher et al., 2010; Kwiatkowski et al., 2020). While bottom-up controls (e.g., nutrient flux, light availability)
have been shown to affect phytoplankton growth in a changing climate, top-down controls (i.e., zooplankton grazing) also play a
role. For example, analysis across a suite of models forced under climate change scenarios revealed grazing pressure as a driver

35   of biomass decline in low to intermediate latitude regions (Laufkötter et al., 2015). Additionally, top-down controls have been
shown to affect regional changes in NPP and export production (Bopp et al., 2001), as well as the timing of phytoplankton
bloom onset (Yamaguchi et al., 2022). Regional redistributions of phytoplankton biomass have consequences for fisheries
management and conservation (Blanchard et al., 2017; Stock et al., 2017), and may have implications for economics and
policy making decisions (Moore et al., 2021).

40   While climate change is known to impact the mean state of phytoplankton biomass or NPP (Bopp et al., 2013; Kwiatkowski
et al., 2020), less is known about how climate change will affect variability in these quantities. One recent modeling study found
that the climate change alters the timing of seasonal blooms in many regions of the global ocean, an effect that could be realized
by the end of the century (Yamaguchi et al., 2022) Several other recent studies have demonstrated how other aspects of the
coupled atmosphere-ocean climate system are projected to experience changes in variance in a changing climate (Resplandy

45   et al., 2015; Landschützer et al., 2018; Kwiatkowski and Orr, 2018; Rodgers et al., 2021). For example, Resplandy et al. (2015)
examined the contribution of internal variability to air-sea pCO_2 and pO_2 fluxes with climate change using a suite of ESMs.
Their analyses revealed distinct regional differences in variability of air-sea pCO_2 and pO_2 fluxes. Other studies have revealed
increases in the frequency of modes of internal variability such as El Niño and La Niña events in response to greenhouse
warming (Timmermann et al., 1999; Cai et al., 2014, 2015, 2022). Clarifying how variance in phytoplankton biomass may be

50   changing over long time scales with climate change is important for fisheries management, especially at regional scales. Near-
term predictions of phytoplankton biomass may also benefit from knowledge of the projected magnitude of internal variability,
as the chaotic nature of internal variability hampers near-term predictions (Meehl et al., 2009, 2014).

Here, we quantify changes in the internal variability (ensemble spread) of phytoplankton biomass over the next century using
a large ensemble of an ESM, in which each ensemble member experiences a different phasing of internal climate variability

55   but is forced with a common emissions scenario. We illustrate the drivers of these changes in variance via statistical analysis
of physical and biogeochemical model output and demonstrate their relative importance in key fisheries regions. While we

recognize that an ESM (and indeed, the real world) is a complex, nonlinear system, we approximate at first-order the linear relationships between key variables to attribute drivers of change in phytoplankton biomass variance.

2 Methods

2.1 Community Earth System Model 1 Large Ensemble

2.1.1 Model Description

We evaluate changes in phytoplankton biomass variance using output from the Community Earth System Model 1 Large Ensemble (CESM1-LE) (Kay et al., 2015). CESM1 is a fully-coupled climate model that simulates Earth's climate under historical and Representative Concentration Pathway (RCP) 8.5 external forcing by simulating the evolution of coupled atmo-sphere, ocean, land, and sea ice component models (Hurrell et al., 2013). The ocean physical model is the ocean component of the Community Climate System Model version 4 (Danabasoglu et al., 2012) and has a nominal 1° resolution and 60 vertical levels. The Parallel Ocean Program version 2 (POP2) ocean model consists of an upper-ocean ecological module which incorporates multi-nutrient co-limitation of nitrate, ammonium, phosphate, dissolved iron, and silicate on phytoplankton growth and dynamic iron cycling (Moore et al., 2004; Doney et al., 2006; Moore and Braucher, 2008). The Biogeochemical Elemental Cycle (BEC) model simulates three phytoplankton functional types (PFTs): diatoms, diazotrophs, and small phytoplankton (i.e., cyanobacteria, nanophytoplankton, picoeukaryotes). Each PFT plays a unique role in the marine ecosystem and occupies a distinct ecological niche. For example, diatoms grow faster in cool, high-nutrient environments while small phytoplankton thrive in warmer, low-nutrient environments. In contrast, diazotrophs are not limited by nitrogen availability due to their ability to biologically fix nitrogen from the atmosphere. Each PFT has a maximum growth rate, which is dictated by temperature (scaled by a temperature function with a Q10 of 2.0), and limited by nutrient and light availability (Moore et al., 2004, 2013). Anthropogenic warming can alter these environmental variables and, in turn, affect phytoplankton abundance and productivity. Photoadaptation (variable chlorophyll to carbon ratios) occurs in response to variations in irradiance and nutrient availability (Geider et al., 1998; Moore et al., 2004). In addition to these bottom-up controls, top-down controls, such as zooplankton grazing, can also affect phytoplankton biomass. The ecosystem model simulates a single generic zooplankton functional type (ZFT) with different grazing rates and half saturation constants prescribed for different PFTs (e.g., slower zooplankton grazing rates for larger phytoplankton i.e., diatoms). Grazing rate is computed using a Holling Type III (sigmoidal) relationship and is a function of both prey density and temperature (Figure S1). Zooplankton loss is a function of a linear mortality term which represents natural mortality and a non-linear predation term which represents losses from predation. Both of these loss terms scale with temperature. While zooplankton growth and loss terms both scale with temperature, a non-linear parameterization of the loss term results in a relatively larger increase in loss than increase in production with warming.

Large ensembles of ESMs are a recently developed research tool which allow us to disentangle fluctuations due to internal climate variability from those imposed by externally forced anthropogenic trends. Internal variability refers to variability in the climate system which occurs in the absence of external forcing, and includes processes related to the coupled ocean-atmosphere

system (e.g., El Niño Southern Oscillation, Pacific Decadal Oscillation) (Santer et al., 2011; Deser et al., 2010; Meehl et al.,
2013). In contrast, external forcing refers to the signal imposed by processes external to the climate system, such as solar
variability, volcanic eruptions, and rising greenhouse gases from fossil fuel combustion (Deser et al., 2012, 2010; Schneider and
Deser, 2018). The CESM1-LE simulates the evolution of the climate system with multiple ensemble members, each initiated
with slightly different atmospheric temperature fields and branched from a multi-century 1850 control simulation with constant
pre-industrial forcing (Lamarque et al., 2010; Danabasoglu et al., 2012). Once the control simulation achieved equilibrium
with the 1850 forcing, ensemble members were integrated from 1920 to 2100 using round-off level differences in the initial
air temperature field (Kay et al., 2015), resulting in each ensemble member experiencing a different evolution of internal
climate variability (e.g., each member has different phasing of climate modes such as El Niño Southern Oscillation). Variable
phasing of internal climate variability across ensemble members can influence phytoplankton biomass variability through the
propagation of physical climate variability to biologically relevant environmental variables. For example, an ensemble member
with a positive phasing of ENSO may display decreased phytoplankton biomass in the Eastern Equatorial Pacific due to
decreased upwelling nutrient flux. RCP8.5 forcing was applied from 2006 to 2100 (Meinshausen et al., 2011) with well-mixed
greenhouse gases and short-lived aerosols projected by four different Integrated Assessment Models (Lamarque et al., 2010). A
total of 40 ensemble members were generated for the CESM1-LE experiment. Six CESM1-LE members had corrupted ocean
biogeochemistry, therefore, we use the 34 CESM1-LE members with valid ocean biogeochemistry.

2.1.2 Statistical Analysis of Model Output

Analyses were conducted using annual mean output at 1° resolution from 1920 to 2100. Changes in CESM1 phytoplankton
variance can be assessed via statistical analysis of chlorophyll concentration, net primary productivity (NPP), or phytoplankton
carbon concentration (an indicator of total biomass). In our analysis we focus on biomass (phytoplankton carbon concentration)
because it is an important predictor variable in offline fisheries models (Christensen and Walters, 2004; Travers-Trolet et al.,
2009; Lehodey et al., 2010; Maury, 2010; Blanchard et al., 2012; Christensen et al., 2015; Jennings and Collingridge, 2015;
Tittensor et al., 2018). Additionally, under climate change scenarios, phytoplankton biomass may be a more reliable indicator
than NPP of climate change impacts (Bopp et al., 2021). Vertical integrals (top 150m) of biomass carbon concentration from
each PFT were calculated and then summed to create maps of total phytoplankton biomass.

We classified the marine environment into 11 ecologically cohesive biomes as in Tagliabue et al. (2021), which are a con-
solidation of the 38 ecological regions defined in Longhurst (2007) using multivariate statistical analysis (Vichi et al., 2011).
Although we consider all 11 biomes in our analysis, we analyze drivers in four biomes that are particularly relevant for fisheries
production and/or of high biogeochemical interest: the subpolar Atlantic (ASP), the subarctic Pacific (SAP), the Equatorial Pa-
cific (EQP), and the Southern Ocean (SOC). ASP is a consolidation of aggregated biogeochemical provinces 4, 11, and 15,
SAP a consolidation of 50 and 51, EQP a consolidation of 61, 62, and 63, and SOC a consolidation of 21, 81, 82, and 83
(Longhurst, 2007; Vichi et al., 2011).
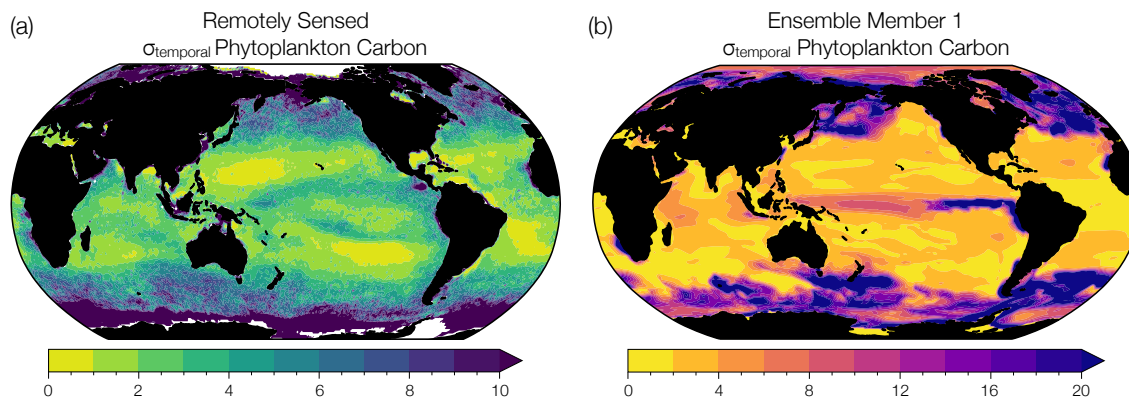
Figure 1. Comparison between observed and modeled phytoplankton biomass interannual variability. (a) Temporal standard deviation in annual mean phytoplankton carbon concentration reconstructed from remotely sensed chlorophyll concentrations, backscattering coefficients, and phytoplankton absorption (1998 to 2019) (Bellacicco et al., 2020) (b) Temporal standard deviation in annual mean phytoplankton carbon concentration simulated by ensemble member 1 of the CESM1-LE over the same observational period (1998 to 2019).

Internal variability at each location (x, y) is approximated as the standard deviation (σ) across ensemble members (EMs) at a given time (t),

$$\sigma(x, y, t) = \sigma(EM(x, y, t)). \qquad (1)$$

The forced response of the large ensemble is calculated as the mean of ensemble members at a given location and time,

$$\overline{LE}(x, y, t) = \frac{\sum_1^n EM(x, y, t)}{n}, \qquad (2)$$

where n is the number of ensemble members.

2.2 Model Evaluation

We used remotely sensed estimates of phytoplankton carbon to evaluate the representation of phytoplankton interannual variability in the CESM1-LE. In other words, we evaluate the temporal variability in modeled phytoplankton biomass from year to year. We note that this interannual variability is different than the internal variability (ensemble spread) that we discuss at length in this study, but is nevertheless a target for model validation. Although phytoplankton carbon concentrations cannot be measured directly by satellites, they can be reconstructed using algorithms that incorporate remotely sensed chlorophyll concentrations, detrital backscattering coefficients, and phytoplankton absorption (Kostadinov et al., 2016; Martinez-Vicente et al., 2017; Roy et al., 2017; Sathyendranath et al., 2020; Brewin et al., 2021). We use the observational phytoplankton carbon

135   dataset of Bellacicco et al. (2020), annually averaged and interpolated onto a 1° grid, to evaluate temporal variability in phytoplankton biomass in a single model ensemble member. Figure 1a shows satellite derived estimates of interannual variability in phytoplankton carbon with regions of relatively low phytoplankton variability shown in light green and regions of relatively high variability in dark blue. Remotely sensed observations capture areas of high interannual variability in the subpolar North Atlantic, North Pacific, and Southern Ocean and areas of low interannual variability in the subtropical gyre regions. Similar

140   spatial patterns are apparent when compared to the range of phytoplankton interannual variability in ensemble member 1 of the CESM1-LE over the observational period (1998 to 2019) (Figure 1b). However, while the model ensemble captures regional patterns of observed variability, the CESM1-LE overestimates the magnitude of observed interannual variability. As such, estimates of interannual variability derived from the model ensemble will tend to overestimate that observed in the real world.

   As an evaluation of the model's ability to represent internal variability (ensemble spread), we compare the internal variance

145   in chlorophyll simulated in the CESM1-LE to a synthetic ensemble generated from observed chlorophyll concentrations over the MODIS remote sensing record (Elsworth et al., 2020, 2021) (Figure S2; chlorophyll was readily available in the CESM1-LE and can be directly compared with our synthetic ensemble of observed chlorophyll). A synthetic ensemble is a novel technique that allows the observational record to be statistically emulated to create multiple possible evolutions of the observed record, each with a unique sampling of internal climate variability (McKinnon et al., 2017; McKinnon and Deser, 2018). Compared

150   to the internal variability over the observational period (2002 to 2020) (purple circle, (Figure S2), the model ensemble slightly overestimates the magnitude of internal variability in chlorophyll observed in the real world.

3   Results

Annually averaged, global mean, upper-ocean (top 150m) integrated phytoplankton biomass across the model ensemble decreases from 76.1 mmol C m^{-2} to 66.2 mmol C m^{-2} from the historical period through the RCP8.5 forcing scenario (1920

155   to 2100), a decline of 13% (black curve; Figure 2a). Phytoplankton biomass declines globally, except in polar regions (Figure 3a). Regional changes in mean phytoplankton biomass across the RCP8.5 forcing scenario (2006 to 2100) display increasing biomass in portions of the Arctic and the Southern Ocean that gradually become ice-free over the century (on the order of 20-40% of the mean biomass across the century) and decreasing biomass across the subtropical gyres (on the order of 15-30% of the mean biomass across the century; Figures 3a, S3a). In the North Atlantic subpolar gyre, the phytoplankton biomass

160   declines by 40-50% of its mean (Figures 3a, S3a), likely due to weakening of the Atlantic Meridional Overturning Circulation (AMOC) and the subsequent disruption of nutrient flux (Brander, 2010). This result is consistent with previous modelling studies which identified a 50% reduction in North Atlantic primary production associated with AMOC weakening during the last glacial period (Schmittner, 2005). A weakening of the AMOC is also projected with anthropogenic warming (Manabe and Ronald, 1993; Stocker and Schmittner, 1997).

165   Regional changes in phytoplankton biomass are dominated by changes in diatom and small phytoplankton (Table 1). We aggregate biomass across 11 ecological provinces (Vichi et al., 2011; Tagliabue et al., 2021), and present changes in total and PFT biomass over the RCP8.5 scenario in Table 1. The CESM1-LE simulates the largest decline in total phytoplankton
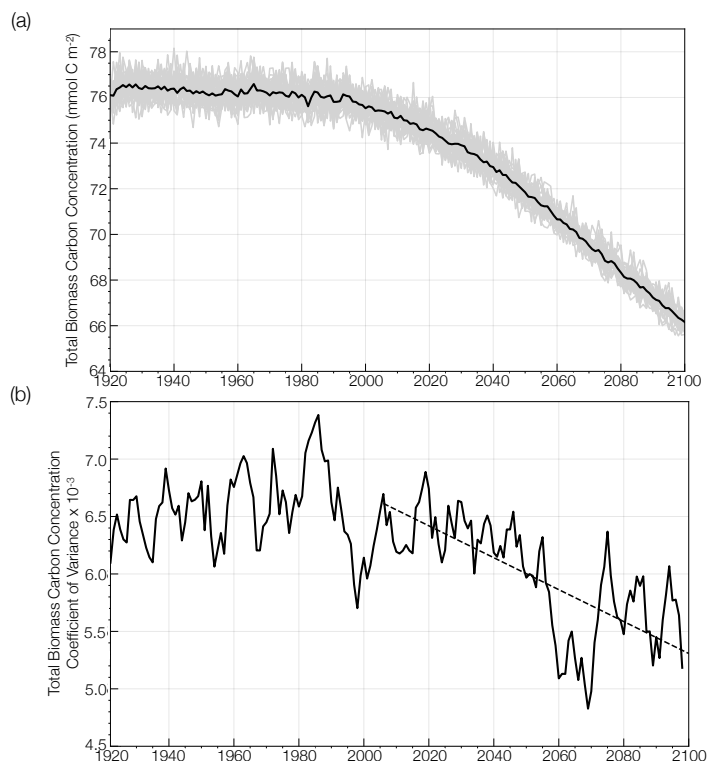
Figure 2. (a) Global change in annual mean total phytoplankton carbon concentration simulated by the CESM1-LE in mmol C m^{-2} from the historical period through the RCP8.5 forcing scenario (1920 to 2100). The ensemble mean is shown in the black curve and the 34 individual ensemble members are shown in the gray curves. (b) Global change in the coefficient of variance in annual mean total phytoplankton carbon concentration over the same period, smoothed using a 5 year window. Trend in the coefficient of variance over the RCP8.5 forcing scenario is shown in the black dashed line.

carbon concentration in the Atlantic subpolar (ASP) region, where diatom biomass declines by ∼80 mmol C m^{-2}, and small phytoplankton biomass increases slightly (∼8 mmol C m^{-2}). We observe moderate decreases in the subpolar Pacific (SAP)
170 region that are again driven by declines in diatom carbon concentration, with minor contributions from changes in small phytoplankton carbon concentration (Table 1). The CESM1-LE simulates a smaller decline in total carbon concentration in the Equatorial Pacific (EQP) region, where diatom biomass declines ∼7 mmol C m^{-2} and small phytoplankton biomass declines ∼5 mmol C m^{-2}. The smallest decline in total carbon concentration occurs in the South Pacific subtropical gyre (SPS) region, where diatom biomass declines ∼4.3 mmol C m^{-2} and small phytoplankton biomass declines ∼4.6 mmol C m^{-2}.
175   Internal variability in global phytoplankton biomass, which is indicated by the spread across the individual ensemble members (gray lines; Figure 2a), declines over the RCP8.5 forcing period from 2006 to 2100. To quantify how the range of internal variability in phytoplankton biomass is changing with anthropogenic warming, we calculated the coefficient of variance as the standard deviation across the ensemble members for a given year (ensemble spread) divided by the ensemble mean. Fig-
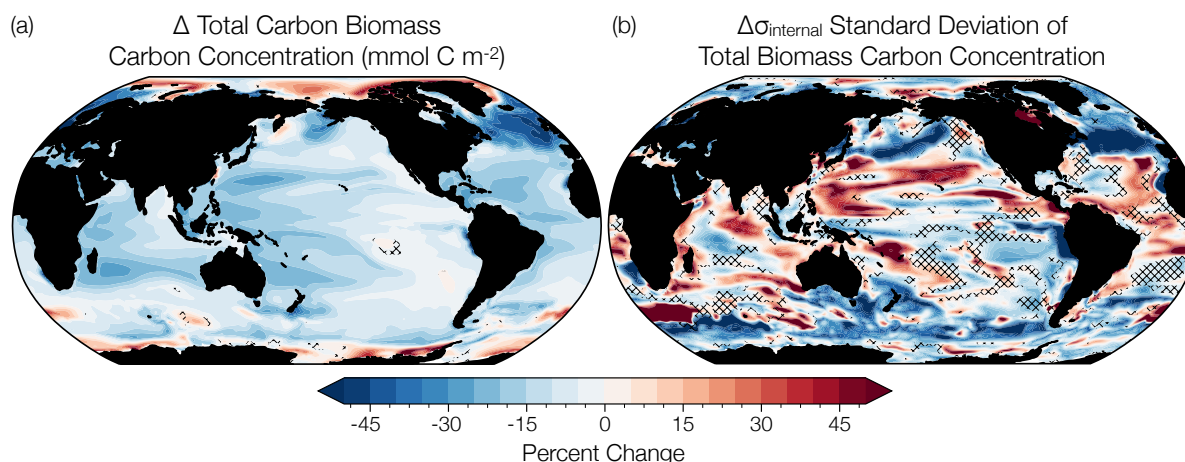
Figure 3. (a) Percentage change in annual total phytoplankton carbon concentration over the RCP8.5 forcing scenario (2006 to 2100) simulated by the CESM1-LE. (b) Percentage change in annual total phytoplankton variablity over the same period. Hatched areas indicate regions of trend insignificance determined by a t-test with a p value greater than 0.05.

ure 2b illustrates the change in the coefficient of variance from the historical period through the RCP8.5 forcing scenario (1920

180 to 2100). The coefficient of variance is relatively constant across the historical period (1920 to 2005), and then significantly declines by ~20% from 2006-2100.

A decrease in global phytoplankton internal variability with anthropogenic warming is not unique to the CESM1-LE. We illustrate this by analyzing phytoplankton chlorophyll (rather than biomass; chlorophyll was readily available in the CMIP5 archive) from three other CMIP5 ESM large ensembles which include representation of ocean biogeochemistry: the GFDL-

185 ESM2M from the Geophysical Fluid Dynamics Laboratory (GFDL; Dunne et al., 2012, 2013), the CanESM2 from the Canadian Centre for Climate Modelling and Analysis (Christian et al., 2010; Arora et al., 2011), and the MPI-ESM-LR from the Max Planck Institute (MPI; Giorgetta et al., 2013; Ilyina et al., 2013), consisting of 30, 50, and 100 ensemble members, respectively. Similarly to the CESM1-LE, historical forcing was applied through 2005, followed by RCP8.5 forcing through 2100. While there is substantial spread in the mean coefficient of variance across the four models, a similar decline in the coeffi-

190 cient of variance can be observed across each of the four ESM ensembles, (Figure S2). From 2006 to 2100, the coefficient of variance decreases by 3.3×10^{-5} yr^{-1} in the CESM1-LE, 2.0×10^{-4} yr^{-1} in the MPI-ESM-LR1, 5.2×10^{-5} yr^{-1} in the CanESM2, and 3.9×10^{-4} yr^{-1} in the GFDL-ESM2M. These declines are statistically significant in all model ensembles with the exception of the MPI-ESM-LR1 (Figure S2).

In comparison to the mean change in phytoplankton biomass, changes in phytoplankton internal variability with time are

195 spatially more heterogeneous across the global ocean (Figure 3b). The largest decreases in variance are apparent in the North Atlantic and North Pacific subpolar regions (on the order of 50-70% of the mean biomass variance), with smaller declines in the Equatorial Pacific and Southern Oceans (on the order of 30-50% of the mean biomass variance) (Figure 3b, S3b). Changes

in variance in the subtropical regions are characterized by mixed trends, with areas of both increasing and decreasing variance across the RCP8.5 forcing scenario (Figure 3b, S3b).

200 Global changes in total phytoplankton biomass variance are a manifestation of changes in diatom and small phytoplankton variability (Table 1). We observe the largest magnitude decline in total phytoplankton carbon variance in the subpolar Atlantic (ASP) region, where diatom variance declines by ~10 mmol C m^{-2} and small phytoplankton variance declines by ~2 mmol C m^{-2} (Table 1). The CESM1-LE simulates a moderate magnitude decline in total phytoplankton variance in the subarctic Pacific (SAP) region, driven by a decrease in small phytoplankton variance (~2 mmol C m^{-2}) with minor contributions from

205 declines in diatom variance (~1 mmol C m^{-2}) (Table 1). Moderate declines in variance are also simulated in the Arctic (ARC), North Atlantic subtropical gyre (NAS), Southern Ocean (SOC), and Equatorial Pacific (EQP) regions, driven by declines in diatom carbon variance in the SOC region and declines in small phytoplankton variance in the EQP region (Table 1).

Table 1. Changes in phytoplankton biomass and its variability in the CESM1-LE from 2006 to 2100 for the 11 ecological provinces defined in Vichi et al. (2011) and Tagliabue et al. (2021). Units are mmol C m^{-2}.

Region		Change in Mean			Change in Standard Deviation		
Biome	Name	Total	Diatom	Small	Total	Diatom	Small
ARC	Arctic	–21	–58	+37	–1.4	–2.8	–0.3
ASP	Atlantic subpolar	–71	–79	+8.2	–5.6	–9.9	–2.2
NAS	North Atlantic subtropical gyre	–18	–15	–2.9	–1.8	–2.8	–0.3
EQA	Equatorial Atlantic	–12	–6.6	–5.9	–0.1	–0.4	+0.2
SAS	South Atlantic subtropical gyre	–10	–7.2	–3.1	–0.5	–0.6	–0.1
IND	Indian Ocean	–11	–6.1	–4.7	+0.1	0	+0.1
SAP	subarctic Pacific	–21	–15	–5.4	–0.1	–1.4	–2.4
NPS	North Pacific subtropical gyre	–11	–5.6	–4.9	–0.2	–0.4	+0.1
EQP	Equatorial Pacific	–12	–6.6	–5.0	–2.0	–2.0	–0.2
SPS	South Pacific subtropical gyre	–8.9	–4.3	–4.6	–0.1	0	–0.1
SOC	Southern Ocean	–9.3	–2.8	–6.6	–1.0	0	–1.3

To guide our attribution analysis of changing phytoplankton biomass and its internal variability, we considered the dominant ecological assemblage across different regions of the global ocean. The CESM1-LE simulates three phytoplankton functional

210 types, each of which thrive in distinct regions of the global ocean. Diatoms dominate in the subpolar Atlantic and Pacific, the Eastern Equatorial upwelling zone, and portions of the Southern Ocean, while small phytoplankton dominate across the subtropical gyres and portions of the Southern Ocean (Figure 4). In contrast, diazotrophs, a minor contributor to total carbon biomass, are present at such low concentrations that they do not dominate anywhere in the global ocean (Figure 4). Using the ecologically cohesive regions defined by Tagliabue et al. (2021) and Vichi et al. (2011), we selected areas that align with

215 the most productive fisheries regions by catch in the Atlantic and Pacific basins (FAO, 2020), as well as regions of global biogeochemical importance for further analysis. In each ecological region we identified the dominant phytoplankton functional
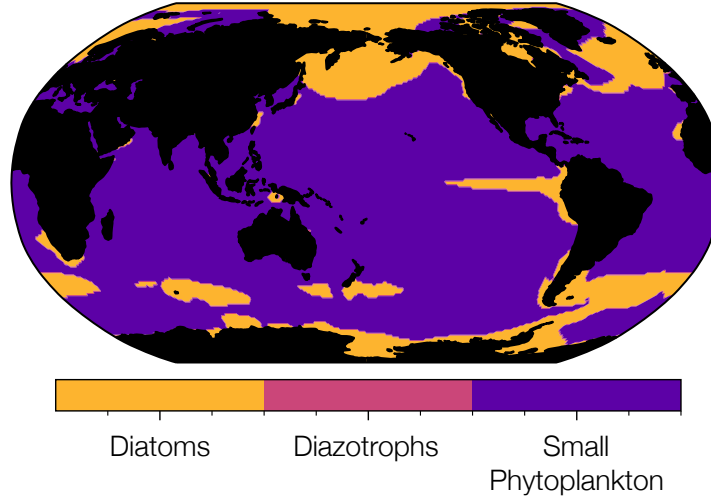
Figure 4. Distribution of the dominant phytoplankton functional type in biomass carbon averaged over 2006 to 2100. The CESM1-LE simulates three phytoplankton functional types: diatoms, diazotrophs, and small phytoplankton. Regions where diatoms dominate are shown in yellow, regions where diazotrophs dominate are shown in pink, and regions where small phytoplankton dominate are shown in purple.

type to include in our driver analysis. In regions where multiple phytoplankton functional types dominated, we used total carbon concentrations to reflect the mixed ecological assemblage.

220   We quantified the relationship between phytoplankton carbon and the variables which contribute to changing phytoplankton biomass and its internal variability by performing a multiple linear regression (MLR) analysis. The MLR analysis was performed on linearly detrended annual anomalies using the ordinary least squares function of the Python package statsmodels.api. We then reconstructed the contribution of each driver variable to phytoplankton biomass and its internal variance between the beginning of the century (2006 to 2016) and the end of the century (2090 to 2100) by multiplying the MLR regression coefficients by the 10-year averaged mean and standard deviation across the model ensemble (ensemble spread), respectively, for

225 each variable. We reconstruct mean phytoplankton biomass ($\overline{C_{phyto}}$) and its variance ($\sigma_{C_{phyto}}$) as a function of light ($Solar$), temperature (SST), phosphate advection ($Nutrient$), mixed layer depth (MLD), and zooplankton grazing ($Grazing$),

$$\overline{C_{phyto}} = \frac{\partial C_{phyto}}{\partial Solar}\overline{Solar} + \frac{\partial C_{phyto}}{\partial SST}\overline{SST} + \frac{\partial C_{phyto}}{\partial Nutrient}\overline{Nutrient} + \frac{\partial C_{phyto}}{\partial MLD}\overline{MLD} + \frac{\partial C_{phyto}}{\partial Grazing}\overline{Grazing}, \tag{3}$$

and,

$$\sigma_{C_{phyto}} = \frac{\partial C_{phyto}}{\partial Solar}\sigma_{Solar} + \frac{\partial C_{phyto}}{\partial SST}\sigma_{SST} + \frac{\partial C_{phyto}}{\partial Nutrient}\sigma_{Nutrient} + \frac{\partial C_{phyto}}{\partial MLD}\sigma_{MLD} + \frac{\partial C_{phyto}}{\partial Grazing}\sigma_{Grazing}, \tag{4}$$

230 where $\overline{X}$ represents the 10-year ensemble mean for a particular variable over a given period, σ_X represents the standard deviation across all ensemble members for a particular variable and $\frac{\partial C_{phyto}}{\partial X}$ represents the MLR regression coefficient describing

the relationship between a particular variable and phytoplankton biomass. We approximate at first-order the linear relation-
ships between variables and do not account for second-order (co-variance among explanatory variables) relationships in our
statistical method; these terms do not contribute much to the total change in mean (Figure S6a) and variance (Figure S6b).

235   We identify the drivers of changing phytoplankton biomass and its internal variance in four distinct ecological regions
using our statistical approach. In the subpolar Atlantic (ASP) and subpolar Pacific (SAP) ecological provinces, where diatoms
dominate total biomass, the mean decline in diatom carbon is associated with a decrease in diatom grazing (Figure S7a) and a
decrease zooplankton carbon, respectively (Figure S7b). In the ASP and SAP ecological provinces (Figure 4), diatom variance
declines between the beginning and end of the century (Figure 5a, b, Table 1). In both provinces, the largest contributions to
240   this decline in diatom variability derive from a decline in diatom grazing variability, while more minor contributions derive
from bottom-up controls such as solar flux, sea surface temperature, nutrient advection, and mixed layer depth (Figure 5a, b).

As the Southern Ocean (SOC) and Equatorial Pacific (EQP) provinces are characterized by mixed phytoplankton assem-
blages where both diatoms and small phytoplankton dominate, we identify the drivers of the change in total phytoplankton
mean and variance here. The mean decline in total carbon in the SOC province are dominated by a decrease zooplankton
245   grazing (Figure S7c). In contrast, drivers of the mean decline in total carbon in the EQP province include a combination of
zooplankton carbon, diatom grazing, and small phytoplankton grazing (Figure S7d).In contrast to the ASP and SAP provinces,
we observe a relatively smaller decline in internal phytoplankton variance between the beginning and end of the century in the
Southern ocean (Figure 5c). Similarly to ASP and SAP provinces, the largest contributions to the change in internal variability
derive from a decline in grazing variability, with bottom-up controls playing only a small role (Figure 5c). In the Equatorial
250   Pacific, total phytoplankton variance declines between the beginning and end of the century, with the largest contributions to
this decline deriving from zooplankton carbon and diatom grazing, with increasing variance in small phytoplankton grazing
(Figure 5d).

We explore the sensitivity of our results in relation to the functional form of grazing in the CESM1-LE (Figure S4). A
caveat to our statistical approach is our assumption that the regression coefficients are constant across the century while the
255   variance is changing. In our model, the sensitivity of grazing rate to prey concentration can be affected by changes in prey
concentration and changes in temperature (Figure S1), both of which are modified in a changing climate. We test the robustness
of our assumption in the two key fisheries regions by performing another MLR to reconstruct drivers of diatom variance with
different regression coefficients between the beginning and end of the century (Figure S1, Figure S4). While the contribution
of zooplankton grazing to the change in diatom variance changes slightly with this new approach, the results are similar.

260   Our analysis reveals that changes in grazer variance dominate the change in phytoplankton variance over the next century,
so we next deconvolve the changes in grazer variance into its two drivers, prey concentration (phytoplankton biomass) and
temperature (Figure S1) using a similar MLR approach as for phytoplankton biomass variance (e.g., Equation 4). The results of
this deconvolution (Figure S8) demonstrate that the changing grazing variance is driven primarily by changing phytoplankton
biomass variance, with only small contributions from changing temperature variance. Thus, it is not possible to cleanly separate
265   cause and effect in this non-linear, coupled system: phytoplankton variance changes because grazer variance changes, and
grazer variance changes because phytoplankton variance changes. Nevertheless, our results suggest that both phytoplankton
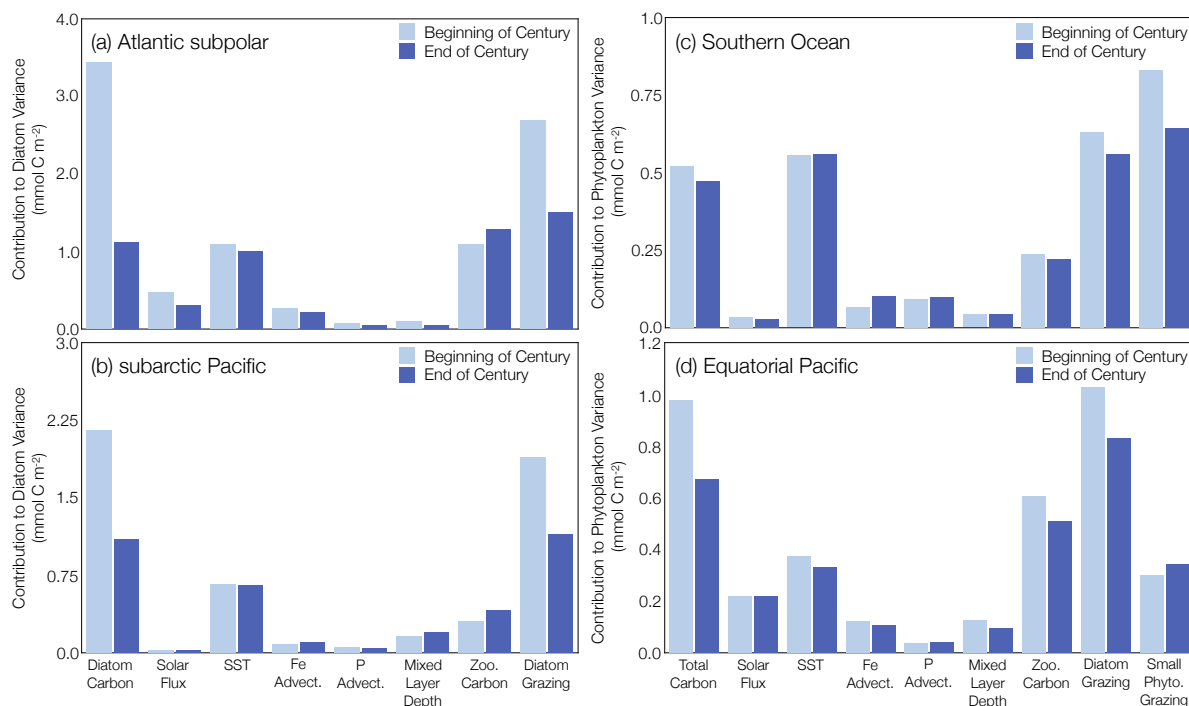
Figure 5. Reconstructed changes in the contribution of each driver variable to phytoplankton biomass variance across the RCP8.5 forcing scenario (2006 to 2100) with the beginning of the century shown in light blue and the end of the century shown in dark blue. Marine ecological regions are defined in Tagliabue et al. (2021). Regions were selected which aligned with the highest fisheries catch in the (a) Atlantic and (b) Pacific basins and the biogeochemically important (c) Southern Ocean and (d) Equatorial Pacific regions. The dominant phytoplankton functional type is considered in each region. In regions with a mixed ecological assemblage, total phytoplankton carbon is considered.

and zooplankton experience declines in variance by the end of the century, and as both are sources of energy for higher trophic levels, this implies that fishery productivity variance will also decline by the end of the century.

4   Conclusions and Discussion

270   We quantify both global and regional changes in phytoplankton internal variance across the RCP8.5, or business-as-usual forcing scenario in the CESM1-LE. We observe a global decline in phytoplankton variance in the model ensemble, which is reflected in similar declines in phytoplankton variance across a suite of CMIP5 models (Figure S2). Regional changes in phytoplankton variability with anthropogenic climate change in the model ensemble are spatially heterogeneous, with highly productive fisheries regions and important global biogeochemical regions experiencing large changes in variance. Statistical

275 analysis of these specific regions reveal zooplankton grazing (top-down control) as an important contributor to changes in phytoplankton variance, consistent with previous studies (Bopp et al., 2001; Laufkötter et al., 2015).

While the CESM1-LE represents regional patterns of observed interannual variability in phytoplankton carbon, the model ensemble tends to slightly overestimate the magnitude of observed internal variance in phytoplankton chlorophyll. As such, the magnitude of changes in phytoplankton internal variance derived from the model ensemble should be interpreted as an

280 overestimate when considering changes in phytoplankton internal variance driven by anthropogenic warming. This caveat is particularly important to consider when interpreting projections from offline fisheries models in the context of fisheries adaptation and planning in a warming climate.

Our statistical approach has inherent limitations, especially in the context of a attributing drivers in an inherently non-linear, coupled system (i.e., reconstructing linear relationships between co-varying variables). In a coupled system such as this, it is

285 difficult to definitively identify cause and effect. In this context, the statistical method can be used as an effective tool to provide a first-order approximation of drivers of phytoplankton variance across the century.

While many studies attribute bottom-up controls to changing phytoplankton with anthropogenic warming (Steinacher et al., 2010; Bopp et al., 2013; Lotze et al., 2019; Tittensor et al., 2021), top-down controls may also play an important role, particularly in our understanding of changing phytoplankton biomass and its variance. Our study demonstrates a key role for

290 top-down controls on changing phytoplankton biomass and its variance in the subpolar North Atlantic and subpolar North Pacific. Previous studies of phytoplankton change with climatic warming have demonstrated that grazing pressure is a driver of biomass decline in low to intermediate latitude regions across a suite of model simulations with different marine ecosystem models (Laufkötter et al., 2015) and that top-down controls can affect regional changes in NPP and export production (Bopp et al., 2001) and is a driver of future shifts in bloom timing (Yamaguchi et al., 2022). While grazing pressure has been shown

295 to increase in response to climate change, several ecosystem models have also identified zooplankton grazing as a dominant driver of phytoplankton assemblage succession during blooms (Hashioka et al., 2012; Prowe et al., 2012a). Additionally, top-down controls have also been observed to affect the onset of the spring bloom (Behrenfeld, 2010; Behrenfeld et al., 2013), to influence primary production in a trait-based ecosystem model (Prowe et al., 2012b).

The relative simplicity of the ocean biogeochemical ecosystem model in CESM1 (e.g., representation of a single zooplankton

300 functional type with multiple grazing rates) may limit a more detailed evaluation of changing grazing pressures with climate change. While the recent parameterization of the biogeochemical ecosystem model in CESM2 (MARBL) includes similar representation of three PFTs and a single adaptive ZFT (Long et al., 2021), more complex configurations of MARBL include explicit representation of additional PFTs such as coccolithophores (Krumhardt et al., 2019) and ZFTs. Using more complex ecosystem models, additional insights into drivers of variability may be gained using our statistical approach. Additionally, the

305 use of an ecosystem model of higher complexity may provide more realistic projections of the marine ecosystem with climate change considering change in phytoplankton and zooplankton species diversity with anthropogenic warming (Benedetti et al., 2021). However, our regional analyses suggest that zooplankton grazing pressure should be considered as an important driver of changes in phytoplankton biomass and its variance with anthropogenic warming.

The magnitude and direction of regional changes in phytoplankton variance are an essential constraint for near-term (sub-
310 seasonal to decadal) predictions of the local marine ecosystem, particularly in important fisheries regions such as the subpolar
Atlantic (ASP) and the subpolar Pacific (SAP) ecological provinces (FAO, 2020). Accurate near-term predictions require fore-
knowledge of both internal climate variability and external climate change signals. On subseasonal to decadal timescales, the
magnitude of internal climate variability is often stronger than forced climate change signals (Meehl et al., 2009, 2014). In
this context, a decline in phytoplankton internal variance with anthropogenic climate change may improve the accuracy of
315 near-term predictions of phytoplankton biomass, producing more reliable forecasts of fisheries productivity. Future work can
utilize these constraints on phytoplankton variance, particularly on regional scales, to inform climate mitigation and adaptation
efforts.

Data availability. CESM1-LE output is available from the Earth System Grid at http://www.cesm.ucar.edu/projects/community-projects
/LENS/data-sets.html.

320 *Author contributions.* GE and NL conceptualized the study. GE analyzed simulation results and prepared the manuscript. N.L. assisted in
preparing the manuscript. KK assisted in analysis of simulation results. TM, KK, and SS assisted in reviewing the manuscript.

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