



Evidence for the Impact of Climate Change on Primary Producers in the Southern Ocean

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Within the framework of the Marine Ecosystem Assessment for the Southern Ocean (MEASO), this paper brings together analyses of recent trends in phytoplankton biomass, primary production and irradiance at the base of the mixed layer in the Southern Ocean and summarises future projections. Satellite observations suggest that phytoplankton biomass in the mixed-layer has increased over the last 20 years in most (but not all) parts of the Southern Ocean, whereas primary production at the base of the mixed-layer has likely decreased over the same period. Different satellite models of primary production (Vertically Generalised versus Carbon Based Production Models) give different patterns and directions of recent change in net primary production (NPP). At present, the satellite record is not long enough to distinguish between trends and climate-related cycles in primary production. Over the next 100 years, Earth system models project increasing NPP in the water column in the MEASO northern and Antarctic zones but decreases in the Subantarctic zone. Low confidence in these projections arises from: (1) the difficulty in mapping supply mechanisms for key nutrients (silicate, iron); and (2) understanding the effects of multiple stressors (including irradiance, nutrients, temperature, pCO₂, pH, grazing) on different species of Antarctic phytoplankton. Notwithstanding these uncertainties, there are likely to be changes to the seasonal patterns of production and the microbial community present over the next 50–100 years and these changes will have ecological consequences across Southern Ocean food-webs, especially on key species such as Antarctic krill and silverfish.

Keywords: phytoplankton, climate, Antarctica, biogeochemistry, deep chlorophyll maximum, ocean colour, MODIS, SeaWiFS

Abbreviations: Chlorophyll-a / chl-a, The ubiquitous light-harvesting pigment in marine phytoplankton usually expressed as a volumetric concentration (mg m⁻³); DCM, Deep chlorophyll maximum, a sub-surface phytoplankton bloom; ENSO, El Niño-Southern Oscillation; HNLC, High nitrate low chlorophyll water; IPCC, Intergovernmental Panel on Climate Change; ISCCP, International Satellite Cloud Climatology Project; MODIS, Moderate Resolution Imaging Spectro-radiometer (NASA); NASA, National Aeronautics and Space Administration of the United States; NPP, Net primary production is defined as the depth-integrated rate of carbon incorporation into organic (living) matter after allowing for respiration of algae (gC m⁻² d⁻¹); PAR, Photosynthetically active radiation (light between 400 and 700 nm); pCO₂, Partial pressure of dissolved carbon dioxide; RCP, Representative Concentration Pathway; SAM, Southern annular mode (a mode of climate variability); SeaWiFS, Sea-viewing Wide Field-of-view Sensor (OrbImage/NASA); VGPM, Vertically-generalised production model.

INTRODUCTION

Primary production by microalgae communities is the foundation of Southern Ocean food-webs (Deppeler and Davidson, 2017; Boyd et al., 2019), providing the organic matter that ultimately sustains Antarctica's unique marine ecosystems (Loeb et al., 1997; Atkinson et al., 2004; Hill et al., 2006; Mock et al., 2017; Boyd et al., 2019; McCormack et al., in review). There are also important feedbacks between the microbial communities and Southern Ocean biogeochemistry, carbon sequestration and the global climate system (Siegenthaler and Sarmiento, 1993; Meskhidze and Nenes, 2006; Sarmiento, 2013; McKinley et al., 2017; Henson et al., 2019; Moreau et al., 2020).

Increases of atmospheric carbon dioxide (CO_2) from $\sim 400 \mu\text{atm}$ today beyond $750 \mu\text{atm}$ by 2100 will likely lead to multifaceted environmental change in the Southern Ocean, including upper-ocean warming, ocean acidification (OA), changes to incident irradiance, increased vertical mixing in the water column, less sea-ice and changed patterns of nutrient input (including iron) (IPCC, 2019; Henley et al., 2020). These environmental and oceanographic changes will affect microbial community composition, patterns of primary production and ecological pathways in Southern Ocean marine ecosystems (Le Quéré et al., 2016; Schofield et al., 2017; Deppeler and Davidson, 2017; Freeman et al., 2019; Johnston et al., in review).

Despite the importance of projecting future changes to primary production and the microbial community composition of the Southern Ocean, current modelling methods have high uncertainty (Leung et al., 2015; IPCC, 2019). The response of the Southern Ocean microbial community to multiple environmental drivers is complex and poorly understood (Petrou et al., 2016; Deppeler and Davidson, 2017). Unlike most of the world's oceans, the vast majority of the Southern Ocean is considered to be replete with nitrate and instead, silicate and iron are limiting in some areas and seasons (Banse, 1996; Boyd et al., 2012, 2001; Hiscock et al., 2003; Doblin et al., 2011). Irradiance can also be crucial to primary production (Deppeler and Davidson, 2017; Kim et al., 2018) and microbial community composition (Arrigo et al., 2010; Kropuenske et al., 2010; Van de Poll et al., 2011; Trimborn et al., 2017) in the Southern Ocean, and irradiance, iron and nutrient availability interact in ways not fully understood at present (Strzepek et al., 2012; Luxem et al., 2017; Trimborn et al., 2019). Further complexities arise from co-limitation by iron and other micronutrients (e.g., Mn; Pausch et al., 2019). Microzooplankton grazing, which can reduce NPP by facilitating nutrient loss through the sinking of particulate detritus (e.g., Cadée et al., 1992; Perissinotto and Pakhomov, 1998; Vernet et al., 2011), will be affected by climate change through changes to grazing rates (Sarmiento et al., 2010; Caron and Hutchins, 2013; Behrenfeld, 2014; Biermann et al., 2015; Cael and Follows, 2016) and phytoplankton nutrient density (Finkel et al., 2010; Hixson and Arts, 2016).

Environmental changes driving these complex biological responses are, in themselves, complex and not well observed. For example, shoaling of the mixed-layer due to decreased vertical mixing can simultaneously increase mixed-layer irradiance, increase grazing, increase ultraviolet-B damage, decrease nutrient

supply, and reduce 'living space' (Garibotti et al., 2005; Vernet et al., 2008; Moreau et al., 2010; Boyd et al., 2014; Zhu et al., 2016; Hoppe et al., 2017; Lloret et al., 2019; Brown et al., 2019; Höfer et al., 2019). However, vertical mixing is not the only iron supply mechanism operating in the Southern Ocean; iron and nutrients (such as silicate) can be introduced into the upper water column by meltwater (from icebergs, sea ice, and glaciers), atmospheric input of iron aerosols, hydrothermal vents, and microbial recycling – Blain et al. (2007), Cassar et al. (2007), Pollard et al. (2009), Boyd and Ellwood (2010), Tagliabue et al. (2010), Treguer (2014), Lannuzel et al. (2016), Boyd (2019), and Hopwood et al. (2019).

Within the framework of the Marine Ecosystem Assessment for the Southern Ocean (MEASO), we present new analyses of the spatial and seasonal patterns of near-surface chlorophyll-a concentration (chl-a) and satellite-based proxies of primary production in the Southern Ocean from Earth-observing satellites, and relate this to information from ships, shore-stations, and autonomous instruments. We consider both primary production in the surface mixed-layer (from the surface to the depth of the seasonal pycnocline, at $\sim 50\text{--}150 \text{ m}$) and in the 'deep chlorophyll maximum' (DCM; Cullen, 2015; Carranza et al., 2018; Uchida et al., 2019). New approaches to track changes in primary production in the DCM based on satellite observations are proposed. Finally, information on future changes to primary producers from global Earth-system models are presented and discussed in the context of our present understanding of the role of multiple-drivers of changes to primary production and our ability to observe, combine and model these drivers.

METHODS

Mixed-Layer Primary Production

Both satellite observations of phytoplankton biomass (proxy of chl-a) and satellite-based models were used to describe recent changes to Southern Ocean net primary production (Table 1). There have been many comparisons between *in situ* and satellite estimates of chl-a in the Southern Ocean. In reprise, some studies conclude that the 'default' (i.e., globally tuned) satellite algorithm for chl-a should be adjusted to improve accuracy in the Southern Ocean (Johnson et al., 2013; Jena, 2017), whereas other studies have found that the default global chl-a algorithm was appropriate for the Southern Ocean (Arrigo et al., 2008; Haentjens et al., 2017; Moutier et al., 2019; Del Castillo et al., 2019). The reduction in absolute uncertainty in chl-a from adjusting the algorithm for the Southern Ocean tends to be small (e.g., Johnson et al., 2013) and the effect on trends will likely be even smaller, so we used the global default chl-a algorithm for SeaWiFS and MODIS-Aqua, and blended these as described in Pinkerton (2019).

For the same period, estimates of NPP are available from two widely used models: the Vertically Generalised Production Model, VGPM, Behrenfeld and Falkowski, 1997) and the Carbon Based Production Model (CBPM, Behrenfeld et al., 2005; Westberry et al., 2008). Alternative primary production

TABLE 1 | Environmental data used in analysis (in alphabetical order).

Variable	Units	Description	Reference(s)
<i>cbpm</i>	mgC m ⁻² d ⁻¹	Net primary production from the Carbon Based Production Model (CBPM). Based on blended SeaWiFS and MODIS-Aqua measurements.	Behrenfeld et al. (2005); ocean.productivity/www.science.oregonstate.edu/ocean.productivity/
<i>chl</i>	mg Chl-a m ⁻³	Near surface concentration of chlorophyll-a from MODIS-Aqua (version R2018.0) and SeaWiFS (version R2018.0) satellite sensors, blended using overlap period 2002–2010 (Pinkerton, 2019).	NASA Goddard Space Flight Center et al. (2018a,b)
<i>kpar</i>	m ⁻¹	Diffuse downwelling attenuation coefficient in the mixed-layer for broadband irradiance, based on blended SeaWiFS and MODIS-Aqua measurements of attenuation at 490 nm (K _D 490)	Clark, 1997; Relationship between K _D 490 and K _{PAR} from Morel et al. (2007).
<i>mld</i>	m	Mixed layer depth calculated from data-assimilating hydrographic model GLBu0.08 hindcast results using a potential density difference of 0.030 kg m ⁻³ from the surface: (1) <i>hycom</i> : from day 265 (2008) to present; (2) <i>fnmoc</i> : from day 169 (2005) to present; (3) <i>soda</i> : from day 249 (1997) to end of 2004; (4) <i>tops</i> : from day 001 (2005) to 225 (2010).	Metzger et al. (2007), Chassignet et al. (2007), and Wallcraft et al. (2009). Data sourced: orca.science.oregonstate.edu/1080.by.2160.monthly.hdf.mld.hycom.php ;
<i>par</i>	μE m ⁻² d ⁻¹	Photosynthetically Active Radiation (PAR) measured as broadband (400–700 nm) incident light intensity at the sea surface as a daily (24 h) average, from blended SeaWiFS and MODIS-Aqua measurements.	Frouin et al. (2012)
<i>seaice</i>	%	Sea ice concentration from the Scanning Multichannel Microwave Radiometer (SMMR) on the Nimbus-7 satellite and from the Special Sensor Microwave/Imager (SSM/I) sensors on the Defense Meteorological Satellite Program's (DMSP) -F8, -F11, and -F13 satellites. Measurements from the Special Sensor Microwave Imager/Sounder (SSMIS) aboard DMSP-F17 are also included. Advanced Microwave Scanning Radiometer - Earth Observing System (AMSR-E) Bootstrap Algorithm with daily varying tie-points.	Cavaleri et al. (1990), updated 2007; https://nsidc.org/
<i>sst</i>	°C	Optimum Interpolation Sea Surface Temperature (OISST), version 2, based on Advanced Very High Resolution Radiometer series (AVHRR) of NOAA (National Oceanic and Atmospheric Administration of the United States).	Reynolds et al. (2002)
<i>vgpm</i>	mgC m ⁻² d ⁻¹	Net primary production from the Vertically Generalized Production Model (VGPM). Based on blended SeaWiFS and MODIS-Aqua measurements.	Behrenfeld and Falkowski (1997) and O'Reilly and Sherman (2016); www.science.oregonstate.edu/ocean.productivity/

models specifically developed for the Southern Ocean have been developed (e.g., Arrigo et al., 2008; Moreau et al., 2015) but data are not widely available and validation is scarce. The accuracy of VGPM and CBPM data in the Southern Ocean is not known, so a (non-exhaustive) review of the existing NPP literature was carried out for preliminary comparison. A total of 573 measurements of (almost exclusively summer) primary production were sourced from 24 studies and each was assigned to a MEASO zone and sector based on geographical location (Table 2) and compared to satellite-based NPP estimates.

Deep-Chlorophyll Maxima

To explore changes in the productivity of phytoplankton at the base of the mixed layer in deep chlorophyll maxima (DCM) we propose a novel metric: irradiance at the base of the mixed layer (E_{DCM} , Equation 2).

$$E_{DCM} = par (1 - \rho_s) \exp(-kpar \cdot mld) \quad (1)$$

Both broadband incident irradiance at the sea-surface (*par*) and diffuse downwelling attenuation (*kpar*) were obtained from satellite observations, and estimates of mixed layer depth (*mld*) were provided from a data-assimilating hydrographic model (Table 1). Based on instrumented elephant seals in the Southern Ocean, Carranza et al. (2018) showed that DCM tends to occur close to the base of the mixed layer defined using a potential

density threshold criterion of 0.03 kg m⁻³. Hence, mixed layer depth (z_m) was obtained from GLBu0.08 hindcast results (sourced from orca.science.oregonstate.edu) using a potential density difference of 0.03 kg m⁻³ from the surface (Metzger et al., 2007; Chassignet et al., 2007; Wallcraft et al., 2009). A constant diffuse sea-surface reflectivity (ρ_s) of 0.07 was assumed (Campbell and Aarup, 1989).

The rationale behind this formulation is that high attenuation in the mixed layer makes it less likely that a DCM is present and vice versa. Essentially, either phytoplankton are distributed relatively evenly through the mixed layer (no DCM, higher mixed-layer attenuation), or are present in a narrow band of elevated concentration at the base of the mixed layer (typically co-located with the nutricline: Cullen, 2015) forming a DCM below a relatively oligotrophic mixed-layer. It is difficult to forecast which of these will occur without good knowledge of the factors involved (*inter alia* water column structure, nutrient supply/demand, incident irradiance, photoadaptive-capability of phytoplankton species present, loss terms including grazing and sinking; Parslow et al., 2001; Kemp et al., 2006; Cullen, 2015; Carranza et al., 2018; Uchida et al., 2019), but we hypothesize that satellite data may be able to tell us which of these situations has occurred after the event.

We recognize that although irradiance at the base of the mixed-layer is likely to be a key factor affecting whether a DCM exists and the level of primary productivity in the DCM (Cullen,

TABLE 2 | Spring-summer integrated net primary production rates ($\text{gC m}^{-2} \text{d}^{-1}$) retrieved from the literature and grouped by MEASO sectors and zones.

Sector	Zone			Global per sector
	Northern	Subantarctic	Antarctic	
Atlantic	NA	0.86 [0.07, 3.02; 89]	0.65 [−0.20, 4.71; 133]	0.74 [−0.20, 4.71; 222]
East Pacific	NA	NA	1.20 [−0.53, 14.5; 154]	1.20 [−0.53, 14.5; 154]
West Pacific	NA	NA	0.94 [0.00, 6.22; 76]	0.94 [0.00, 6.22; 76]
Central Indian	0.34 [0.15, 0.95; 20]	0.44 [0.00, 1.02; 29]	0.51 [−0.13, 3.83; 72]	0.46 [−0.13, 3.83; 121]
East Indian	NA	NA	NA	NA
Global per zone	0.34 [0.15, 0.95; 20]	0.75 [0.00, 3.02; 118]	0.88 [−0.53, 14.5; 435]	

Bold numbers represent mean values, while square brackets contain minimum and maximum rate as well as the number of values retrieved from the literature, respectively. Literature consulted: Saijo and Kawashima (1964), El-Sayed and Mandelli (1965), Mandelli and Burkholder (1965), Horne et al. (1969), El-Sayed (1970), El-Sayed and Taguchi (1981), El-Sayed et al. (1983), von Bodungen et al. (1986), Smith and Nelson (1990), Verlenca et al. (1990), Holm-Hansen and Mitchell (1991), Karl et al. (1991), Helbling et al. (1995), Savidge et al. (1995), Moline and Prézélin (1997), Figueiras et al. (1998), Saggiomo et al. (1998), Bracher et al. (1999), Dierssen et al. (2000), Varela et al. (2002), Uitz et al. (2009), Hoppe et al. (2017), Aracena et al. (2018), and Höfer et al. (2019).

2015), productivity and biomass of phytoplankton at depth will be affected by other factors, such as phytoplankton composition, nutrient concentrations and temperature (Sallée et al., 2015). In addition, mixed layers can contain vertical structure in optical properties (Carranza et al., 2018). To evaluate the utility of E_{DCM} as an indicator of DCM, a comparison was made between E_{DCM} and the amount of phytoplankton biomass in the DCM from three Southern Ocean Carbon and Climate Observations and Modeling (SOCOMM project; Riser et al., 2018; Uchida et al., 2019) profiling drifters between 2013 and 2018. Phytoplankton biomass in the DCM was proxied from these float measurements as the depth-integrated phytoplankton carbon biomass (C_p) minus the surface phytoplankton carbon biomass multiplied by the mixed layer depth, $C_p(\text{surf})$, following Uchida et al. (2019).

Spatial Summaries

Spatial variability in primary productivity was summarised using the MEASO spatial framework (Constable et al., in review; **Supplementary Information**). Briefly, MEASO defines five longitudinal sectors, three latitudinal zones (Northern between Subtropical and Subantarctic fronts; Subantarctic between Subantarctic and Southern Antarctic Circumpolar Current (ACC) fronts; and Antarctic south of Southern ACC front), and 15 areas from the sector-zone intersects.

Environmental Change in the Southern Ocean

Although autonomous profilers are delivering increasingly powerful datasets (e.g., Boyer et al., 2013; Buongiorno Nardelli et al., 2017; Uchida et al., 2019), large-area (Southern Ocean scale) and long-term (decadal) observations of environmental change in the Southern Ocean are predominantly from Earth-observation satellites (e.g., Cavalieri et al., 1990; Reynolds et al., 2002; Haentjens et al., 2017; Del Castillo et al., 2019), sometimes in conjunction with data-assimilating hydrodynamic models (e.g., Metzger et al., 2007; Chassignet et al., 2007; Wallcraft et al., 2009). To describe the oceanographic and environmental setting, this study focused on 4 key environmental data sets for which large-area, spatially resolved and long-term information is available (**Table 1**): sea-surface temperature

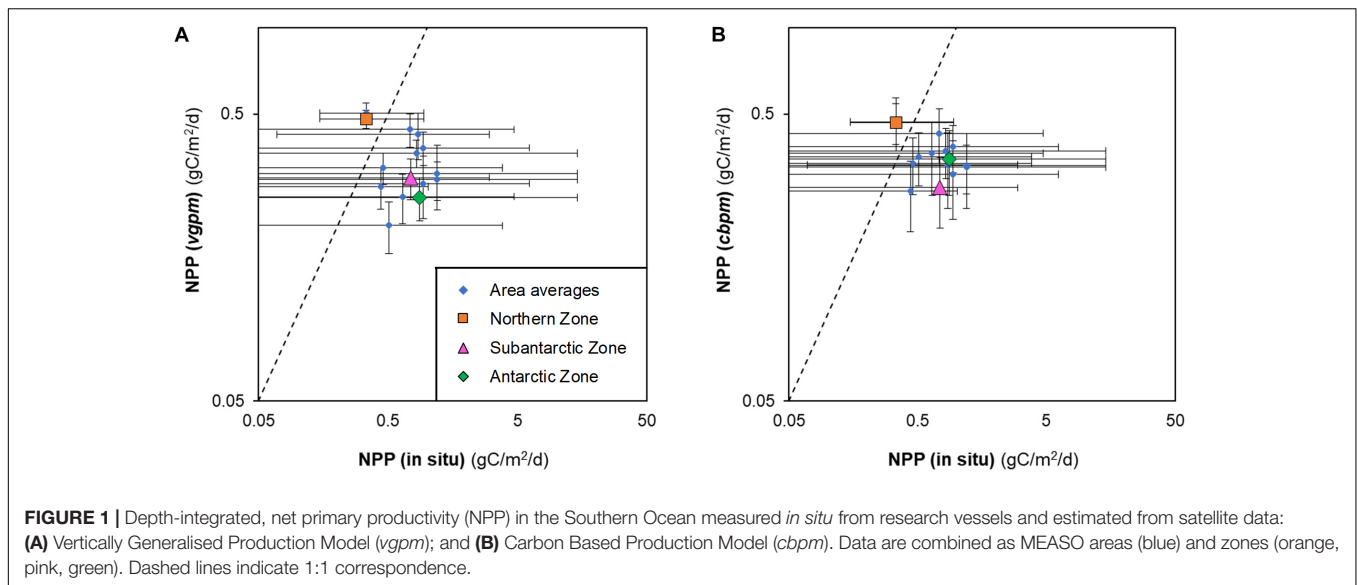
(*sst*); sea ice concentration (*ice*); mixed layer depth (*mld*); and photosynthetically active radiation at the sea surface (*par*). Together, these describe major environmental drivers of change in the Southern but clearly do not capture all factors relevant to primary production, including nutrient supply mechanisms, acidification and grazing.

Statistical Analyses

Linear trends in monthly anomalies (differences from climatological means) for each dataset (*chl*, *sst*, *ice*, *mld*, *par*, *vgpm*) at the pixel level (smallest sampling scale) were determined using the Sen slope (Sen, 1968). This value is the median slope of all pairs of points in the time series. The insensitivity of the Sen slope to outliers means that it is generally the preferred non-parametric method for estimating a linear trend (Hipel and McLeod, 1994). Seasonal trends were calculated using anomalies from three months (spring: September–November; summer: December–February; autumn: March–May; winter: June–August).

The Sen slope was also used to describe trends at the scale of MEASO zones, sectors and areas. Satellite-based estimates of *chl-a* and NPP fail at low solar elevations, and we have not attempted to “fill in” the winter gaps in satellite data (e.g., as Park et al., 2019). The proportion of missing data increases with latitude and so to avoid any potential bias in area-averages, trends were only calculated when more than half of potential observations for an area were present. The statistical significance of trends was assessed using the non-parametric Mann-Kendall test (Mann, 1945; Kendall, 1975) which does not require a normal distribution assumption. We used the method of Yue and Wang (2004) to adjust the effective number of degrees of freedom for autocorrelation.

The influence of four environmental drivers (*sst*, *ice*, *mld*, *par*) on *chl-a* was considered by a multiple linear regression (Equation 1), where the coefficients minimize the sum of squares of the error (ϵ). This analysis was not applied to satellite estimates of primary production (*vgpm*, *cbpm* or E_{DCM}) to avoid circularity: satellite measurements of *chl-a* are independent of observations of these environmental drivers but *vgpm*, *cbpm* and E_{DCM} are not. Here, *chl* is the monthly anomaly in *chl* (and similarly for



other variables).

$$\widetilde{chl} = \alpha_0 + \alpha_1 \widetilde{sst} + \alpha_2 \widetilde{ice} + \alpha_3 \widetilde{mld} + \alpha_4 \widetilde{par} + \varepsilon \quad (2)$$

An approximation to the contribution to overall trend (Sen slope) in chl-a from each candidate driver variable (*sst*, *ice*, *mld*, *par*) is given as the product of the respective linear coefficient (α) and the trend (Sen slope) of the variable. The analysis was carried out in IDL 8.5 (Research Systems Inc., Boulder, CO, United States).

RESULTS

Mixed-Layer Primary Production

Although our compilation of *in situ* measurements of depth-integrated NPP from research vessels and shore-stations was not exhaustive, it nevertheless shows a clear pattern of where primary production has been measured more often to date (Table 2) and highlights the need to improve knowledge of primary productivity in the entire East Indian sector as well as the Subantarctic and Northern zones where data are scarce or non-existent. The paucity of the NPP data meant that no robust conclusions could be drawn as to the relative accuracies of VGPM and CBPM. Both NPP models look to be overestimating NPP in the Northern zone by a similar amount of ~40% (Figure 1) and underestimating NPP in the Subantarctic and Antarctic zones by $55 \pm 15\%$ (mean $\pm$ standard deviation).

Satellite observations (Figure 2A) show that chl-a was generally higher in Subantarctic areas, lower south of the Polar Front and that there were some areas of elevated productivity south of the southern limit of the ACC (especially in the Ross Sea and Bellingshausen Sea/western Antarctic Peninsula). Patterns of primary productivity estimated from satellite observations (Figures 2C,E) generally followed those of chl-a (higher values in Subantarctic waters and over the Antarctic shelf) but there was a strong positive dependence of NPP on latitude. There were

also significant differences in spatial variations of annual-average *vgpm* compared to *cbpm*, with *vgpm* higher to the north of the region, and *cbpm* higher to the south.

Increasing trends in chl-a between 1997–2019 were detected by satellites in most Northern and Subantarctic zones (Figure 2B). In contrast, decreasing trends in chl-a were observed in most Antarctic continental shelf-sea waters, especially in the Ross Sea, Weddell Sea and Prydz Bay, except along the western Antarctic Peninsula. Trends in *vgpm* (Figure 2D) closely followed those in chl-a. Seasonal trend analysis of chl-a and *vgpm* (see Supplementary Information) shows predominantly positive trends in autumn and negative trends (over the Antarctic shelf) in summer. Trends in *cbpm* were negative throughout the Southern Ocean (Figure 2F), including in Northern and Subantarctic zones in contrast with *vgpm*. Seasonal analysis of trends in *cbpm* suggests that changes in productivity in the summer drive these overall trends.

In terms of environmental drivers of changes in chl-a, we found that only a small amount (mean 5.6%, 5th–95th percentile range 0.9–16.8%) of the monthly anomalies in chl-a over the last 20 years was explained by a linear combination of *sst*, *ice*, *mld* and *par* (Figure 3). The proportions of variance explained by the individual drivers were less than 2%, with *sst* explaining most and *par* the least. The linearized contribution to the trends in chl-a from these individual environmental drivers (Figure 4) showed little spatial structure and were typically small, less than $0.001 \text{ mg m}^{-3} \text{ y}^{-1}$, whereas the trends in chl-a were up to $\sim 0.01 \text{ mg m}^{-3} \text{ y}^{-1}$ in some areas of the Southern Ocean.

Deep-Chlorophyll Maxima in the Southern Ocean

The regression between irradiance at the base of the mixed layer and the amount of phytoplankton biomass in the DCM from three SOCCOM floats (Figure 5) was highly significant ($F_{95} = 82.7$, $p < 0.001$) with about half of the variance explained ($R^2 = 0.47$).

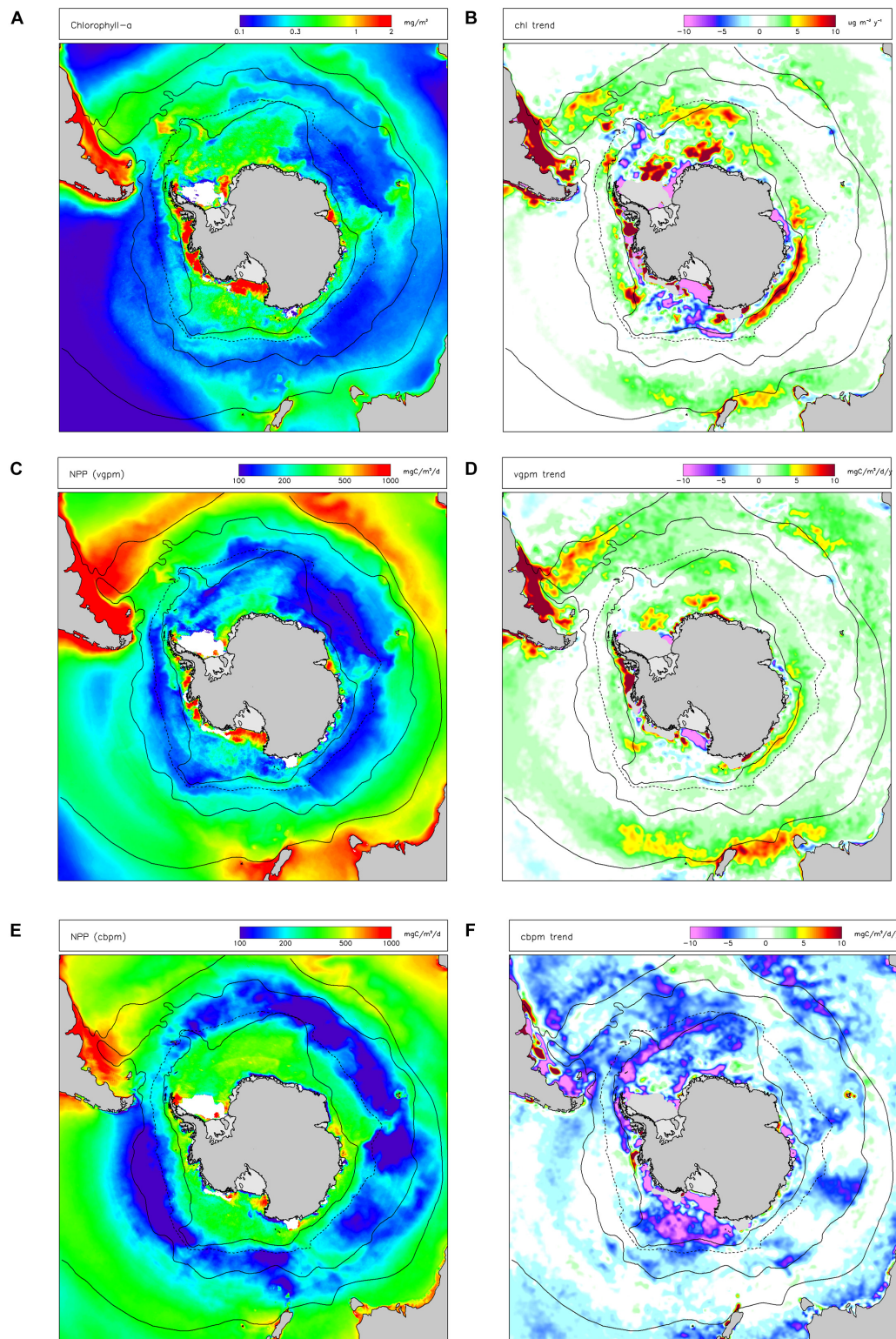
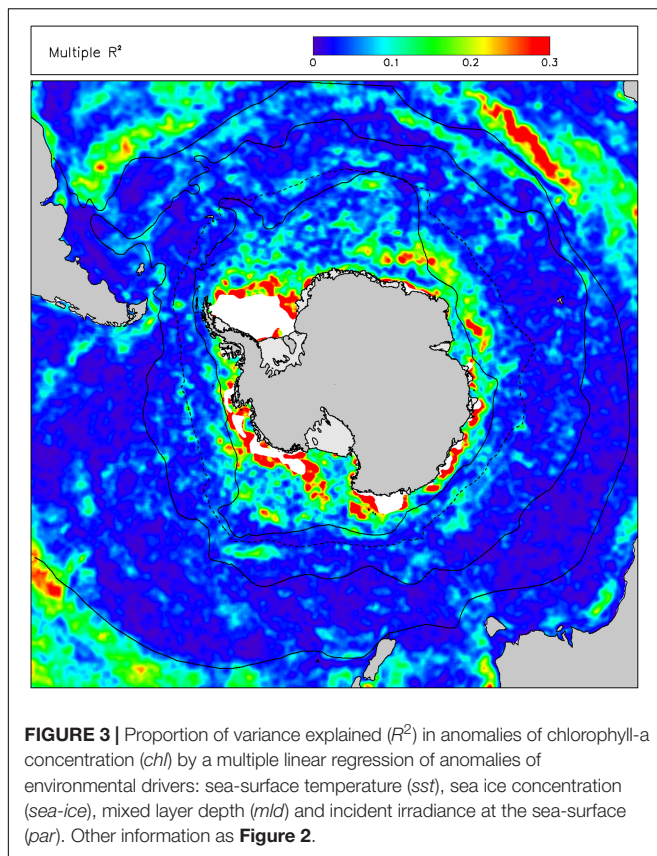


FIGURE 2 | Long-term (1997-2019) mean values of indicators for primary production: **(A)** chlorophyll-a concentration (chl); **(C)** net primary production in the water column estimated by the VGPM algorithm ($vgpm$) and the CBPM algorithm ($cbpm$) **(E)**. Linear trends (Sen slopes) over the same period are shown for **(B)** chl ; **(D)** $vgpm$; **(F)** $cbpm$. White indicates missing data. Black lines are nominal positions of (from north): Subtropical Front (STF, solid line), Subantarctic Front (SAF, solid line), average maximum northern extent of seasonal sea ice (dashed line), and the Southern boundary of the Antarctic Circumpolar Current (SB-ACC, solid line).



Average E_{DCM} values were low through most of the Southern Ocean except in a band close to the southern boundary of the ACC and especially in the Atlantic and Central Indian sectors (**Figure 6A**). High values of mean E_{DCM} were also found in parts of the Northern zone of the Pacific sector. Trends in E_{DCM} (**Figure 6B**) were negligible north of the northern limit of seasonal sea ice, and almost exclusively negative south of this. Decreasing trends in E_{DCM} were greatest between longitude 0° and 60° (Atlantic and Central Indian sectors) and occurred almost exclusively during the summer months (December–February; see **Supplementary Information**).

Trends Summary by MEASO Areas

Significant increasing trends in *chl-a* and *vgpm* between 1997–2019 were found in all MEASO zones and sectors except for *chl-a* in the Antarctic zone (**Table 3**). Increases were highest in the Atlantic and West Pacific sectors. Significant increasing trends were also found for many (*chl-a*) or most (*vgpm*) MEASO areas. Positive trends in *vgpm* were almost exclusively greater in magnitude and more significant than trends in *chl-a* (with the exception of AON and WPA areas). In contrast, all significant trends in *cbpm* were negative, and were highest in Subantarctic and Antarctic zones. For the Southern Ocean as a whole, the mean trend and significance in *vgpm* was $0.8\% \text{ y}^{-1}$ ($p < 0.0001$) compared to $0.5\% \text{ y}^{-1}$ for *chl* ($p = 0.002$), whereas the overall Southern Ocean trend in *cbpm* was negative ($-0.5\% \text{ y}^{-1}$) but not significant ($p = 0.17$). Significant trends in irradiance at

the base of the mixed-layer (E_{DCM}) over the same period were exclusively negative, and substantially larger than trends in *chl-a* and *vgpm* especially in the Subantarctic and Antarctic zones and in the Atlantic sector (trends $> 5\% \text{ y}^{-1}$ in magnitude). At the scale of the Southern Ocean, the Sen slope in E_{DCM} was highly significant $-3.2\% \text{ y}^{-1}$ ($p < 0.0001$). Plots of time series by zones, sectors and area, and full statistics on trend analysis are given in **Supplementary Information**.

DISCUSSION

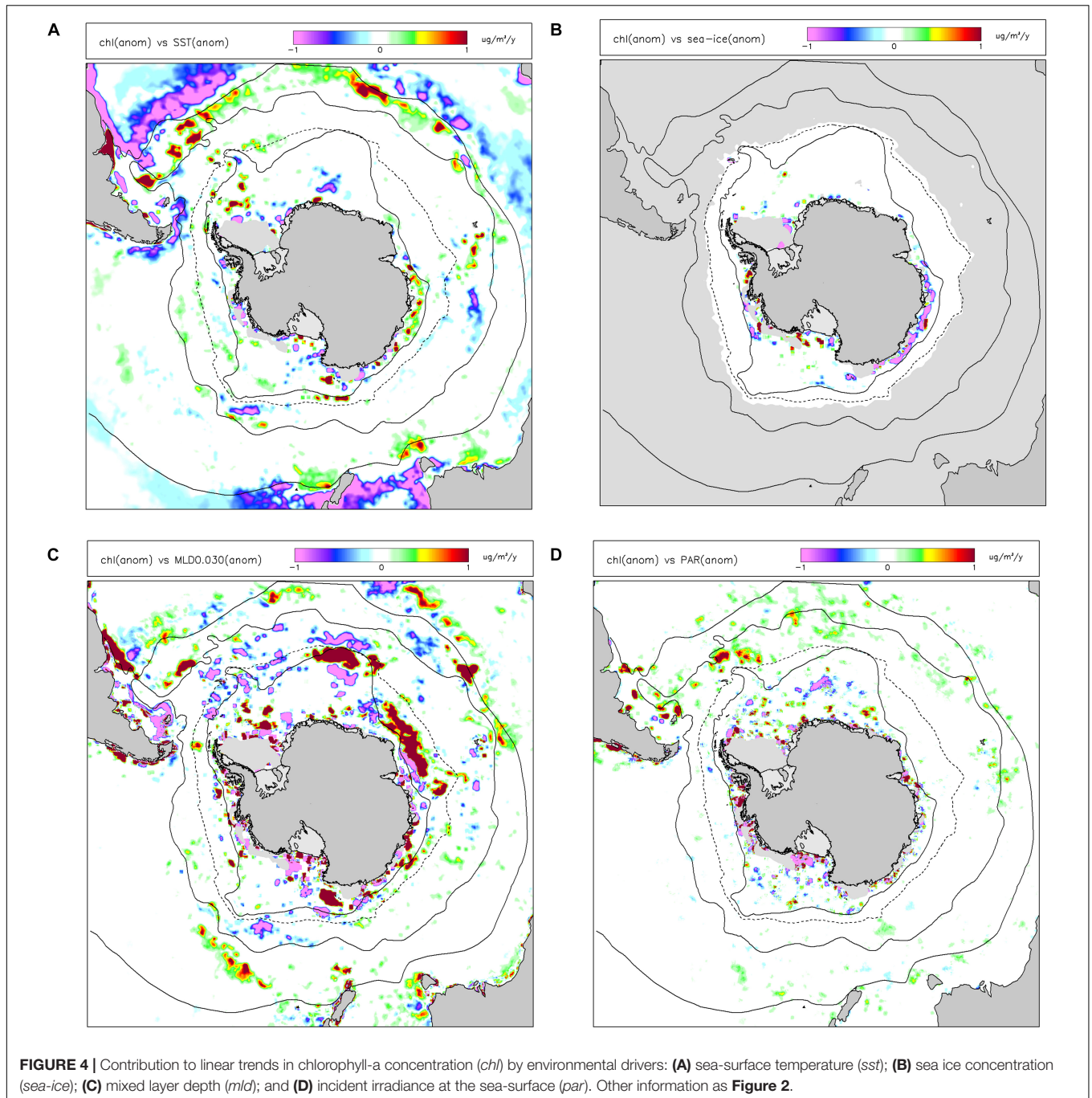
Mixed-Layer Primary Production

The present study found that *chl-a* and NPP were higher in the Atlantic sector than in other sectors of the Southern Ocean, likely as a result of higher iron availability due to land proximity (de Baar et al., 1995; Banse, 1996), and productivity was also elevated around the Kerguelen Plateau and Balleny Islands, consistent with enhanced supply of iron and major nutrients to surface waters (Blain et al., 2007). Annual-average values of *chl-a* and NPP were also high in some parts of the Antarctic zone, especially Prydz Bay (CIA), Ross Sea (WPA), and Bellingshausen Sea/western Antarctic Peninsula (EPA), likely because of persistent polynyas (Arrigo et al., 2015).

In terms of trends in *chl-a*, our results agreed with Del Castillo et al. (2019) who found statistically significant increases in *chl-a* in all sectors of the Southern Ocean, with an especially strong increase in the Northern and Subantarctic zones. Primary production in these zones are seasonally limited by the availability of silicate availability, a constraint which favours phytoplankton communities made up of small flagellates coccolithophores, cyanobacteria, and dinoflagellates (Wright et al., 2010; Balch et al., 2011; Freeman et al., 2019). In these areas, upper-ocean warming in conjunction with higher $p\text{CO}_2$ was anticipated to increase phytoplankton primary production (Steinacher et al., 2010; Boyd, 2019) which agrees with positive trends observed in *chl-a* (**Figure 2**).

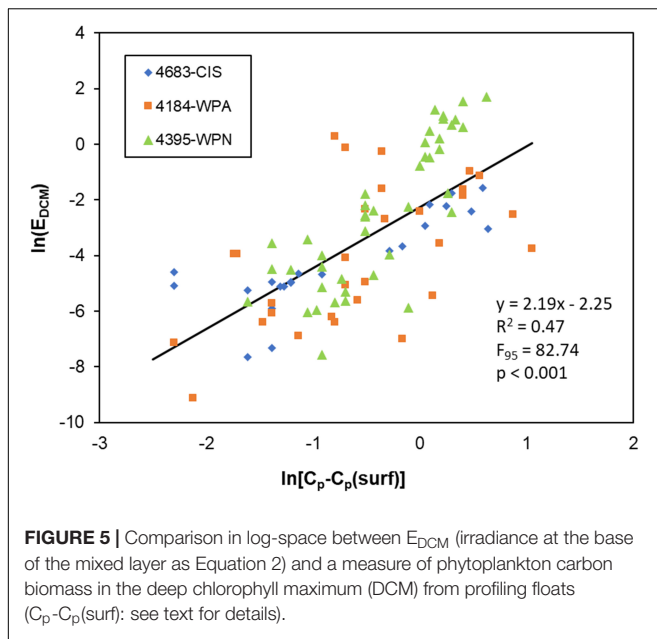
Further south, silicate-rich waters in the southern Subantarctic and Antarctic zones tend to favour diatom-dominated communities (Petrou et al., 2016; Balch et al., 2016; Rembauville et al., 2017; Nissen et al., 2018; Trull et al., 2018), and here we found the trends in *chl-a* to be more mixed, with both increases and decreases over the last few decades. The Ross Sea was the main Antarctic area with negative trends in *chl-a*, but we are not aware of *in situ* measurements to confirm this.

To date, the most consistent long-term observations of phytoplankton and factors affecting primary production have been made from coastal research stations, notably along the coastal West Antarctic Peninsula as part of the Long Term Ecological Research Network (LTER; Montes-Hugo et al., 2009; Moreau et al., 2015; Kim et al., 2018; Brown et al., 2019). Over the 20-year LTER record, Kim et al. (2018) found significant positive trends in *chl-a* at some field stations on the Antarctic Peninsula but decreasing phytoplankton biomass at others. Our study shows increases in *chl-a* along the West Antarctic Peninsula (**Figure 2**) but the spatial scale of the satellite data is coarser and unreliable within a few km of the shore. Brown et al.



(2019) found that increasing upper ocean stability along the West Antarctic Peninsula between 1993–2017 due to a combination of wind, sea ice and meltwater dynamics, led to enhanced primary production, especially of diatoms. It appears that local-scale forcing (e.g., changes to sea ice, glacier melting, changes to coastal current patterns), and large-scale climate cycles like El Niño Southern Oscillation (ENSO) and SAM both affect long-term change in Antarctic coastal productivity (Montes-Hugo et al., 2009; Schloss et al., 2014; Kim et al., 2018; Brown et al., 2019; Höfer et al., 2019).

It is notable that trends from *vgpm* were predominantly positive throughout the Southern Ocean whereas trends in *cbpm* were almost exclusively negative (compare **Figures 2D,F**). The *vgpm* data are based on *chl-a*, so it is expected that trends in *chl* and *vgpm* agree, whereas *cbpm* is based on satellite estimates of the C:Chl ratio and does not use *chl-a* *per se*. The paucity of *in situ* measurements of NPP in the Southern Ocean (see **Table 2**) means that we cannot empirically compare the accuracy of *vgpm* versus *cbpm*, or carry out independent trend analysis, but we note that the assumption of nitrate-limited phytoplankton



production implicit in *vgpm* is unlikely to be valid for the Southern Ocean, so *cbpm* may simply be more reliable than *vgpm*. Alternatively, the different patterns of change in chl-a (and *vgpm*) compared to *cbpm* may be associated with a change in community composition. Laboratory and shipboard experiments show that the responses of phytoplankton to environmental changes such as these will be species-specific (Hoppe et al., 2013, 2017; Alvain and d'Ovidio, 2014; Trimborn et al., 2017; Andrew et al., 2019; Strzepek et al., 2019). We speculate here that whereas *vgpm* is essentially showing trends in phytoplankton biomass (via the proxy of chl-a), *cbpm* could also be responding to changes in the microbial community, at least in terms of size classes. Decreases in *cbpm* compared to *vgpm* in the Southern Ocean would be consistent with a shift towards smaller phytoplankton species at high latitudes at the expense of larger species, in line with some predictions (e.g., Rouseaux and Gregg, 2015; Petrou et al., 2016; Deppeler and Davidson, 2017; Trimborn et al., 2017) and observations (e.g., Moline et al., 2004), although changes in size structure vary spatially and with climatic variability such as SAM and ENSO (Montes-Hugo et al., 2008). Higher scattering efficiencies of smaller species would likely lead to lower satellite-estimates of Chl:C ratios and tend to give lower estimates of growth rates (μ) by the *cbpm* (Behrenfeld et al., 2005). This suggestion is unproven and warrants further research.

It is increasingly clear that the response of phytoplankton to multiple stressors acting concurrently cannot be obtained by superimposing their separate responses (Boyd and Brown, 2015; Zhu et al., 2016; Boyd et al., 2016; Luxem et al., 2017; Andrew et al., 2019; Strzepek et al., 2019; Trimborn et al., 2019; Boyd, 2019). Satellite observations in the Southern Ocean show complex patterns of environmental change; surface warming in much of the Northern zone contrasts with slight cooling trends over the last 40 years further south (Maheshwari et al., 2013; Kostov et al., 2016; Sallée, 2018); average sea ice concentration

has decreased in the Amundsen Sea but increased in parts of the Weddell, Bellingshausen and Ross Seas (Vaughan et al., 2013; Zhang et al., 2018; Pinkerton, 2019; IPCC, 2019); irradiance at the sea-surface has increased north of the Subantarctic Front and generally reduced to the south over the last 20 years; over the same period, mixed-layer depths have likely shallowed in the Northern zone, and both deepened and shallowed in different parts of the Subantarctic and Antarctic zones (Leung et al., 2015; Pinkerton, 2019).

Given the multifaceted and non-linear response of phytoplankton to these environmental changes, it is perhaps unsurprising that the linear model with 4 forcing factors (*sst*, *ice*, *mld* and *par*) explained only a small fraction (5.6%) of the variance in chl-a over the Southern Ocean (Figure 3), and the individual environmental contributions to chl-a trends were negligible (Figure 4). Also, we recognize that satellite observations were not available for important factors including ocean pH, pCO_2 , and grazing, so these factors were not included as drivers in our empirical analyses of recent changes to chl-a.

Based on long-term sampling from research stations in the Antarctic peninsula region, Kim et al. (2018) showed that variability in chl-a is strongly linked to large-scale climate cycles (ENSO and SAM). Analyses of biogeochemical models are also providing similar insights into these climate-biology relationships acting over large areas (e.g., Hauck et al., 2015). Given the important effects of multi-decadal climate variability such as ENSO and SAM on patterns of primary production, Henson et al. (2010) estimated that ~40 years of continuous satellite ocean-color data was needed to reliably ascribe any trends in chl-a and production to climate change rather than variability. Del Castillo et al. (2019) repeated the analysis for the Atlantic sector of the Southern Ocean and found that ~34 years of continuous data were needed. We caution therefore that the satellite record is still not long enough to separate long-term trends from climate variability.

Deep Chlorophyll Maxima (DCM)

Deep chlorophyll maxima (DCM) can form and persist over several months in the Southern Ocean depending on factors including the state of the seasonal pycnocline and nutricline, rates of nutrient supply, incident irradiance, photoadaptation, grazing and sinking (Parslow et al., 2001; Kemp et al., 2006; Cullen, 2015; Carranza et al., 2018; Uchida et al., 2019). Phytoplankton in the DCM have elevated pigment concentrations, likely indicative of production being light-limited, though iron and silicic acid limitation may also be present (Parslow et al., 2001). The factors affecting when, where and how a deep phytoplankton bloom develops have been extensively studied (review by Cullen, 2015), and although observations generally agree with established hypotheses, the lack of accurate information on key drivers mean that forecasts of DCMs are unreliable (Uchida et al., 2019). For this reason, we presented a new approach to tracking changes in DCM in the Southern Ocean. Based on data from three SOCCOM floats in the Southern Ocean, about half the

TABLE 3 | Annual average mean values and long-term linear trends (1997–2019) for: phytoplankton biomass (chl-a concentration); net primary production (NPP) by the vertically-generalised production model (VGPM) and carbon-based production model (CBPM); and irradiance at the base of the mixed-layer (E_{DCM}) proxy of primary production in the deep chlorophyll maximum (DCM).

	Chl-a		NPP (VGPM)		NPP (CBPM)		E_{DCM}	
	mean	trend	mean	trend	mean	trend	mean	trend
	mg m ⁻³	% y ⁻¹	mgC m ⁻² d ⁻¹	% y ⁻¹	mgC m ⁻² d ⁻¹	% y ⁻¹	μE m ⁻² d ⁻¹	% y ⁻¹
Southern Ocean	0.20	0.5**	222	0.8***	164	−0.5	0.10	−3.2***
Zones								
Northern	0.20	0.6***	294	0.7***	199	−0.2	0.12	−0.6*
Subantarctic	0.19	0.4*	168	0.7***	107	−1.3*	0.04	−5.4**
Antarctic	0.36	0.3	200	0.9***	223	−1.0	0.51	−5.1**
Sectors								
Atlantic	0.28	0.7*	258	1.0***	175	−0.8	0.04	−6.6***
Central Indian	0.20	0.4**	212	0.6***	125	−0.8*	0.02	−3.2**
East Indian	0.18	0.5*	223	0.7**	127	−0.4	0.04	−0.7
East Pacific	0.14	0.4**	178	0.7***	188	−0.2	0.31	−1.9***
West Pacific	0.19	0.6**	242	0.9***	191	−0.3	0.20	−0.2
Areas								
AON	0.29	0.8***	416	0.7***	242	−0.2	0.04	−0.4
AOS	0.27	0.6	204	0.8**	131	−1.7**	0.03	−8.7***
AOA	0.34	0.4	165	1.1**	193	−1.2	0.23	−7.1***
CIN	0.21	0.3*	331	0.4***	154	−0.4	0.02	−0.7*
CIS	0.18	0.4*	169	0.6***	104	−1.4*	0.03	−3.6**
CIA	0.25	0.9	157	1.4***	264	−0.3	0.74	−5.2**
EIN	0.19	0.5	299	0.6**	112	0.0	0.01	0.3
EIS	0.16	0.4	162	0.6***	132	−0.9	0.04	−2.0
EIA	0.32	1.3	180	1.7*	285	−0.4	0.49	−3.6
WPN	0.17	0.9***	281	1.0***	224	0.1	0.16	0.0
WPS	0.17	0.2	162	0.6**	103	−1.5*	0.03	−6.0**
WPA	0.40	−0.6	209	0.2	205	−2.1*	0.33	−2.7
EPN	0.12	0.4***	202	0.6***	229	−0.2	0.27	−1.3***
EPS	0.14	0.3	137	0.5*	81	−0.8	0.06	−7.0**
EPA	0.47	0.5	245	1.0	256	−1.1	0.68	−3.8**

The magnitude of the trend is expressed as a proportion of the mean value (% year⁻¹). Significance of the trend (Mann-Kendall linear trend test corrected for autocorrelation) is shown: * $p \leq 0.05$ ** $p \leq 0.01$ *** $p \leq 0.001$.

variability in the amount of phytoplankton biomass in the DCM was explained by our simple metric of irradiance at the base of the mixed layer (E_{DCM}). The comparison shown in **Figure 5** provides preliminary support for E_{DCM} being a useful metric for tracking changes in DCMs in the Southern Ocean.

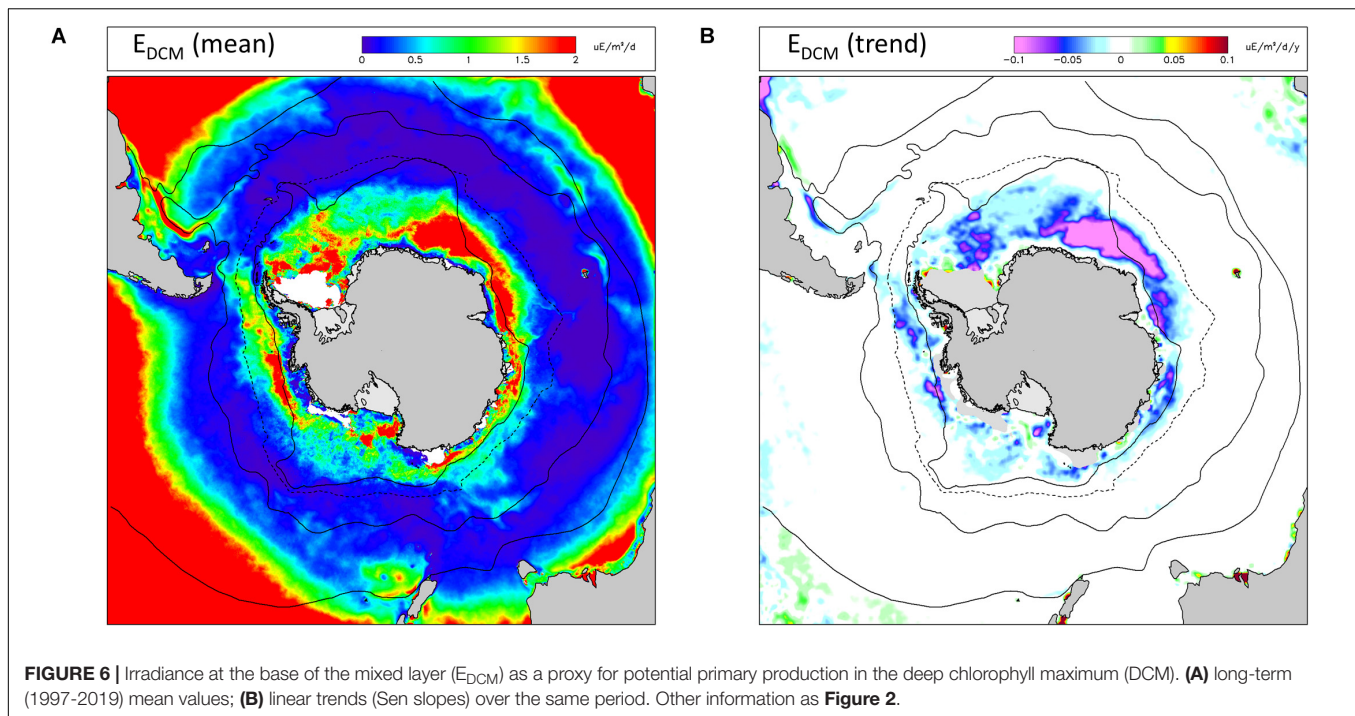
The new E_{DCM} metric revealed a significant decrease in NPP at depth in the Antarctic sector of the Southern Ocean (**Figure 6**), but there were not co-located hotspots of trends in chl-a, diffuse irradiance attenuation, or mixed layer depth. The interpretation is that relatively small changes over time to attenuation and mixed-layer depth acting together can lead much more significant trends in E_{DCM} . Further analysis of this preliminary result is recommended as variations in DCMs could have important consequences for ecosystems and biogeochemistry because of higher efficiencies of organic matter export from sub-surface primary production (Tilstone et al., 2017; Henley et al., 2020).

PROGNOSES FOR THE FUTURE

Mixed-Layer Primary Productivity

Based on Earth-systems models, the ‘Special Report on the Ocean and Cryosphere in a Changing Climate’ (IPCC, 2019; Meredith et al., 2019) included a summary of observed changes in NPP and drivers, and projected future changes. Future projections were based largely on the CMIP5 (Coupled Model Intercomparison Project) which used two Representative Concentration Pathways (RCPs): RCP2.6 (low greenhouse gas emission, high mitigation future) and RCP8.5 (high greenhouse gas emission scenario, ‘business as usual’, in the absence of policies to reduce climate change). Key conclusions from CMIP5 model projections of NPP (Leung et al., 2015; Meredith et al., 2019) were as follows:

- In the Northern MEASO zone, higher mean underwater irradiance (from reduced mixed-layer depths) and higher iron supply were projected. Overall, this projection points to increased primary production in the mixed-layer and



increased phytoplankton biomass (Leung et al., 2015; Meredith et al., 2019). These model projections are consistent with recent observations provided in the current study (chl-a, *vgpm*) and elsewhere (e.g., Le Quéré et al., 2005; Doney, 2006; Del Castillo et al., 2019).

- In the Subantarctic zone, deeper summertime mixed-layer depth together with increased cloud albedo were projected to lead to lower average irradiance in summer, leading to lower chl-a and NPP (Leung et al., 2015). This result agreed with a modelling study by Moore et al. (2018) which found that changes to sea ice and circulation patterns under climate warming scenarios would lead to a global reorganization of nutrient distributions and a steady decline in global-scale marine biological production. However, recent satellite observations show recent increasing rather than decreasing trends in chl-a in this zone (Del Castillo et al., 2019; present study).
- In the Antarctic zone, CMIP5 models generally suggested that less seasonal sea ice and a warming ocean will lead to greater iron supply, higher underwater irradiance and thence to increases in chl-a and NPP (Leung et al., 2015; Rickard and Behrens, 2016). These projected increases agree with recent trends in chl-a and *vgpm* (present study), except in the Ross Sea where chl-a, *vgpm* and *cbpm* all show negative trends.

Confidence in future projections of chl-a and NPP remains low (IPCC, 2019). The strongest drivers of future changes in NPP in CMIP5 models were iron availability and irradiance; acidification and temperature *per se* were less important (Leung et al., 2015). The balance between

different iron-supply mechanisms (i.e., vertical mixing *versus* aeolian *versus* ice-mediated supply) are hence crucial to our ability to forecast future changes to the productivity of the Southern Ocean (Boyd et al., 2012; Boyd et al., 2014; Leung et al., 2015; Hutchins and Boyd, 2016; Hopwood et al., 2019). High spatial and seasonal variability in the relative importance of various iron-supply mechanisms, coupled with a lack of long-term observations, the simultaneous change of a number of environmental conditions, and the complexities of phytoplankton response to different environmental drivers hence severely limit our ability to anticipate these changes (Hutchins and Boyd, 2016; Mongwe et al., 2018; Freeman et al., 2019; Smith et al., 2019; Hopwood et al., 2019). In the longer term, longer-time series of satellite observations, increasingly sophisticated laboratory experiments, and more co-ordinated and extensive Antarctic observations such as the Southern Ocean Observing System (SOOS) are expected to help provide the information required to improve these future projections (Newman et al., 2019).

Deep Chlorophyll Maxima (DCM)

Prognoses of future changes in production in the DCM in the Southern Ocean are not reliable and Earth system models focus instead on depth-integrated estimates of NPP (e.g., Leung et al., 2015; IPCC, 2019). Better satellite-based observation of the occurrence of DCMs in the Southern Ocean using the simple metric described here (E_{DCM}) and better *in situ* observations using autonomous technology could improve this situation in the future. In particular, the advent of biogeochemical Argo floats (Rembauville

et al., 2017; Briggs et al., 2018; Carranza et al., 2018), the SOCOMM project (Riser et al., 2018; Uchida et al., 2019) and Southern Ocean and Climate (SOCLIM) floats¹ represent a major step forward.

Primary Production by Sea Ice Algae

Although not a focus of the present study, we note that tracking and anticipating changes to primary production in the Southern Ocean should include that within sea ice (Arrigo, 2014; Saenz and Arrigo, 2014; van Leeuwe et al., 2018) and beneath it (Arteaga et al., 2020). Although sea ice algae only contribute ~1% of total Southern Ocean primary production, and 12–50% of total primary production in the sea ice zone (Kottmeier et al., 1987; Grossi et al., 1987; Saenz and Arrigo, 2014; van Leeuwe et al., 2018), sea ice algae are of disproportionate ecological importance because their production occurs in locations and at times when production in the water column is low (Quetin et al., 1996; Saenz and Arrigo, 2014; McCormack et al., in review). As such, sea ice algae are a crucial bridge between low and high productivity periods for many mid-trophic level species, such as Antarctic krill (*Euphausia superba*; Daly, 1990; Smetacek et al., 1990; Loeb et al., 1997; Kohlbach et al., 2017; Meyer et al., 2017), and Antarctic silverfish (*Pleuragramma antarctica*) (Guglielmo et al., 1998; Vacchi et al., 2004).

Drivers of primary production by sea ice algae include ice-extent and thickness, incident light availability, and nutrient supply (Kottmeier and Sullivan, 1990; Arrigo et al., 1998; Arrigo, 2014; Hobbs et al., 2016; Tedesco and Vichi, 2014), though temperature and salinity can be important (Tedesco and Vichi, 2014; Saenz and Arrigo, 2014). Variations in snow depth will influence both light penetration into sea ice, and nutrient input (Saenz and Arrigo, 2014). Both laboratory manipulations and *in situ* experiments indicate that sea ice algae are little affected by changes to pH (McMinn, 2017).

Complex models have been developed to simulate the large-scale primary production by sea ice algae (Arrigo et al., 1991, 1997; Arrigo and Sullivan, 1994; Saenz and Arrigo, 2012; Arrigo, 2014; Tedesco and Vichi, 2014) but these have neither been well validated to date (Meiners et al., 2012) nor used to investigate long-term changes in sea ice algae primary production. Furthermore, no future projections of changes to sea ice algae production are available in CMIP5 models (IPCC, 2019).

In the longer term (~100 years hence) it is likely that sea ice algae primary production will decrease in line with reducing sea ice extent and concentrations throughout the Southern Ocean (IPCC, 2019), but these changes are likely to be spatially heterogeneous and non-linear (van Leeuwe et al., 2018). We also note that the ecosystem consequences of a reduction of primary production in sea ice could be significant and far reaching (Atkinson et al., 2004; Meyer et al., 2017; Saenz and Arrigo, 2012; Arrigo, 2014; Tedesco and Vichi, 2014; McCormack et al., in review) so this represents a major gap in forecasting capability.

¹<http://soclim.com/index.php>

SUMMARY FOR POLICY MAKERS

Summary Tables

A summary of recent observed changes and anticipated future changes (Table 4 and Figure 7) shows that primary production in the Southern Ocean will likely increase over the next 100 years, with more primary production in the water column and less in sea ice. The distinctive nature of the microbial community of the Southern Ocean (i.e., the dominant species of phytoplankton, phenology (seasonality) and spatial distribution of primary production) will likely reduce, with shifts towards communities more dominated by small and flagellated species, and with endemic Southern Ocean phytoplankton species losing out to temperate species (Deppeler and Davidson, 2017). Year-to-year variability in primary production in the Southern Ocean will likely increase with increasing prevalence of marine heatwaves (Oliver et al., 2019). Recent increases in sea ice concentration (and potentially associated sea ice algae production) will likely reverse in the next few decades and decrease consistent with less ice in a warming Southern Ocean (IPCC, 2019). The importance of local-scale forcing means that forecasting the effects of climate change on coastal primary production, crucial to the reproductive success of many endemic Antarctic species, is especially challenging (Montes-Hugo et al., 2009; Kim et al., 2018). The effects of future changes to primary production are likely to be greatest for those Southern Ocean species with life-cycles intimately linked to seasonal sea ice growth and retreat, including ‘keystone’ species such as Antarctic krill and silverfish (Smetacek et al., 1990; Quetin et al., 1996; Loeb et al., 1997), and their predators (McCormack et al., in review).

Key Messages for Policy Makers

KM1

Satellite observations show mainly increases in phytoplankton biomass in the Southern Ocean over the last 20 years (1997–2019) (*high confidence*), but the direction of recent changes to primary production are generally not known except to say that it is likely that primary production has decreased in the Ross Sea over the recent past (*medium confidence*).

KM2

At present the satellite record is not long enough to separate long-term trends from climate variability, so we cannot say whether these observed trends will continue in the future (Henson et al., 2010; Del Castillo et al., 2019) (*high confidence*).

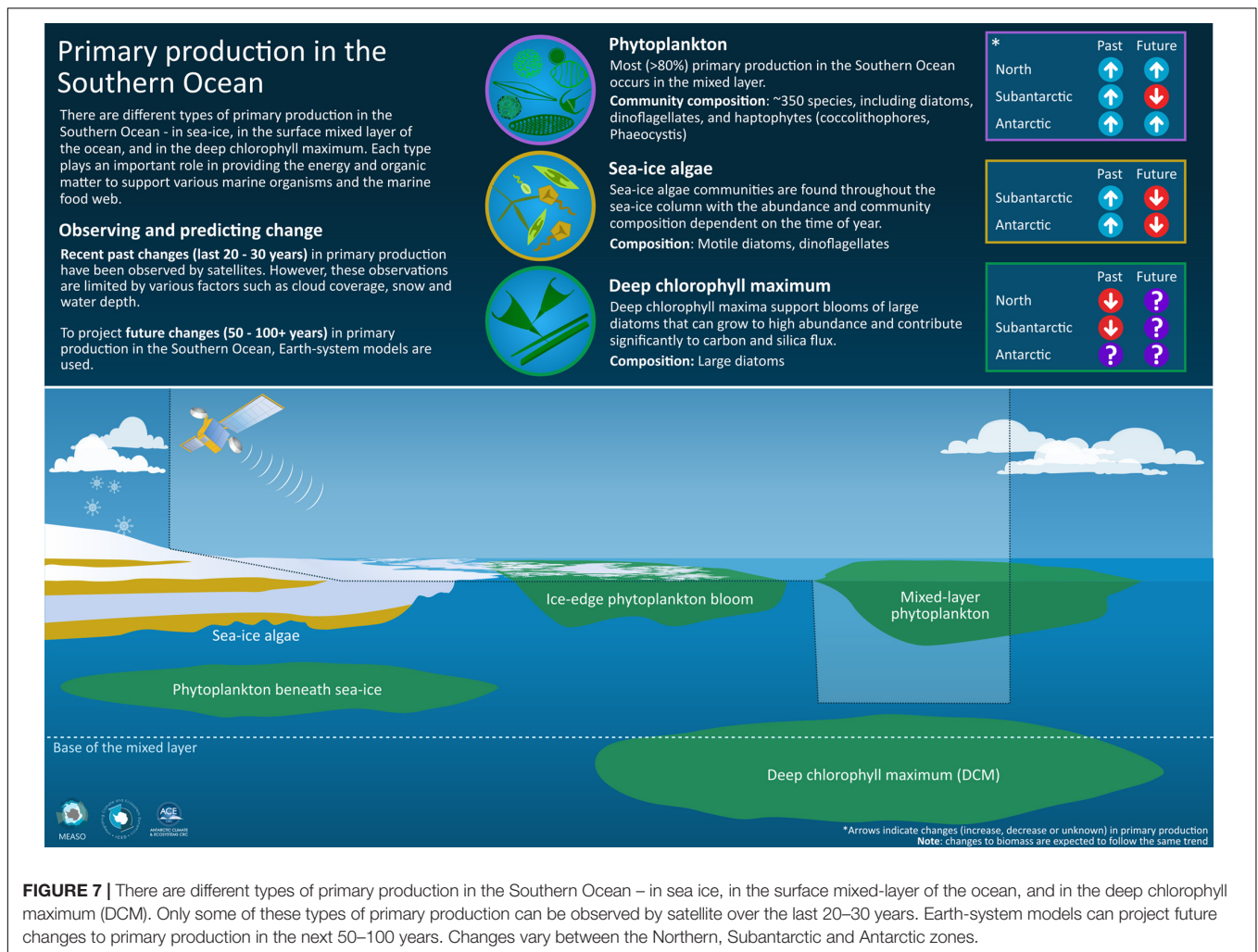
KM3

Over the next 100 years, Earth system models project increasing primary production in the northern and Antarctic MEASO zones but decreases in the Subantarctic zone (Leung et al., 2015; Rickard and Behrens, 2016) (*low confidence*). Low confidence in these projections arise from the difficulty in mapping supply mechanisms for the key nutrients of iron and silicate in the Southern Ocean and understanding the effects of multiple stressors on different species of Antarctic phytoplankton

TABLE 4 | Summary of recent observed changes (satellite data) and future projections by MEASO areas of the Southern Ocean.

Sectors	Recent observed trends				Future projections		
	Zones				Zones		
	Northern	Subantarctic	Antarctic	All zones	Northern	Sub-antarctic	Antarctic
Atlantic	↗↗--	↘↘↘	↘↗↘	↗↗↘	↑	↓	↑
Central Indian	↗↗↘	↗↗↘	↘↗↘	↗↗↘	↑	↓	↑
East Indian	↘↗--	↘↗--	↘↗--	↗↗--	↑	↓	↑
West Pacific	↗↗--	↘↘↘	↘↘↘	↗↗--	↑	↓	↑
East Pacific	↗↗↘	↘↗↘	↘↘↘	↗↗↘	↑	↓	↑
All sectors	↗↗↘	↗↗↘	↘↗↘	↗↗↘	↑	↓	↑

Arrows show recent trends, in order: phytoplankton biomass in the mixed-layer (chl-a concentration, 1997–2019, chl); net primary production (NPP, 1997–2019) by Vertically Generalised Production Model (vgpm) and by Carbon Based Production Model (cbpm); irradiance at base of the mixed-layer (1997–2019, E_{DCM}). The arrows show: ↑ indicates a significant increasing trend $> 1\% \text{ y}^{-1}$; ↗ significant increasing trend $< 1\% \text{ y}^{-1}$; – no significant trend over the period analysed; ↘ significant decreasing trend $< 1\% \text{ y}^{-1}$; ↓ significant decreasing trend $> 1\% \text{ y}^{-1}$. So, for example, “↘↗↘” indicates no trend in chl, strongly increasing trend in vgpm, decreasing trend in cbpm, and no trend in E_{DCM} . ‘Future projections’ are based on CMIP5 models (Leung et al., 2015; **Figure 1**) just for NPP: ↑ increases projected for the future; – no changes (or a mixture of increases and decreases) projected; ↓ decreases projected for the future.

**FIGURE 7 |** There are different types of primary production in the Southern Ocean – in sea ice, in the surface mixed-layer of the ocean, and in the deep chlorophyll maximum (DCM). Only some of these types of primary production can be observed by satellite over the last 20–30 years. Earth-system models can project future changes to primary production in the next 50–100 years. Changes vary between the Northern, Subantarctic and Antarctic zones.

(Hutchins and Boyd, 2016; Boyd et al., 2016, 2019; Deppeler and Davidson, 2017; Freeman et al., 2019; Meredith et al., 2019; Trimborn et al., 2019).

KM4

As well as affecting the total amount of primary production in the Southern Ocean, climate change will likely alter seasonal patterns in production (phenology) and the relative abundances of different types of phytoplankton (Wright et al., 2010; Petrou et al., 2016; Balch et al., 2016; Kaufman et al., 2017; Nissen et al., 2018; Trull et al., 2018) (*high confidence*). These changes will affect zooplankton, have ecological consequences across Southern Ocean food-webs including on keystone species and top predators (Atkinson et al., 2004; Moline et al., 2004; Pinkerton and Bradford-Grieve, 2014; Johnston et al., in review; McCormack et al., in review) (*high confidence*).

KM5

Primary production by sea ice algae will likely decline in the future as sea ice extent shrinks (*medium confidence*). Because of the ecological importance of sea ice to a range of key Southern Ocean species, the reduction in Southern Ocean sea ice and its associated primary production could lead to a critical tipping point in Southern Ocean ecosystems (*medium confidence*).

KM6

Better methods of monitoring change to phytoplankton and sea ice algae are needed to improve confidence in future projections of primary production in the Southern Ocean (*high confidence*). Efforts to maintain long-term coastal observations (e.g., Palmer Long Term Ecological Research Network LTER, e.g., Kim et al., 2018), improve satellite observations, co-ordinate field sampling, and develop and deploy autonomous instrumentation in the Southern Ocean are essential to assess long-term trends (Newman et al., 2019) (*high confidence*). Long-term, multi-trophic level monitoring is required to understand the effects of changes to primary production on middle and upper level predators such as krill, salps, fish, seabirds and marine mammals (*high confidence*).

FREQUENTLY-ASKED QUESTIONS (FAQ)

What is primary production and why is it important?

Primary production is the formation of organic matter by photosynthesis. It is the process by which energy enters the marine food-web. All marine animals ultimately rely on organic matter created by primary production.

Why can't satellites see ice algae?

Ice algae typically grow within or below sea ice, so that the sea ice stops satellites seeing the colour of the algae directly.

How does climate change affect primary production?

Primary production depends primarily on the amount of light available and on the concentration of nutrients in sea-water. If the amount of cloud cover, sea ice or snow changes, this affects the amount of light entering the water column. The depth of mixing in the ocean also affects the light availability. Many processes affect nutrient supply, including those associated with water column mixing, dust input, circulation patterns, icebergs, snow and sea ice. There are lesser effects on phytoplankton due to warming, acidification, carbon dioxide concentration and indirect effects from changes to zooplankton grazers.

Why is it so hard to predict what will happen to phytoplankton?

There are many different species of phytoplankton in the Southern Ocean and all respond differently to environmental changes. The effects of multiple stressors acting on species at the same time also makes it difficult to anticipate phytoplankton responses to global change.

Why do the predictions vary with location?

Ocean physics differ drastically among regions of the Southern Ocean, which means that environmental changes in the Southern Ocean are not the same everywhere. For example, some areas are warming and other cooling; some areas have more ice and some less. Also, phytoplankton communities are not the same everywhere, and different species respond to environmental change in different ways.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: <https://oceandata.sci.gsfc.nasa.gov/>, <http://sites.science.oregonstate.edu/ocean.productivity/>, <https://nsidc.org/>, <https://www.ncdc.noaa.gov/isccp>.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.592027/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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