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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, pCO_2, 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); pCO_2, 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 ~400 μatm today beyond 750 μatm 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 (Sarmento 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; Llort 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 ~50–150 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)
cbpm	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/
chl	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)
kpar	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_D490)	Clark, 1997; Relationship between K_D490 and K_{PAR} from Morel et al. (2007).
mld	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) *hycom*: from day 265 (2008) to present; (2) *fnmoc*: from day 169 (2005) to present; (3) *soda*: from day 249 (1997) to end of 2004; (4) *tops*: 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;
par	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)
seaice	%	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.	Cavalieri et al. (1990), updated 2007; https://nsidc.org/
sst	°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)
vgpm	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 scare. 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).

$$E_{DCM} = par\,(1 - \rho_s)\exp\left(-kpar \cdot mld\right) \tag{1}$$

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 (gC m^{-2} 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), Verlencar et al. (1990), Holm-Hansen and Mitchell (1991), Karl et al. (1991), Helbling et al. (1995), Savidge et al. (1995), Moline and Prézelin (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(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 a 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, $\widetilde{chl}$ is the monthly anomaly in *chl* (and similarly for

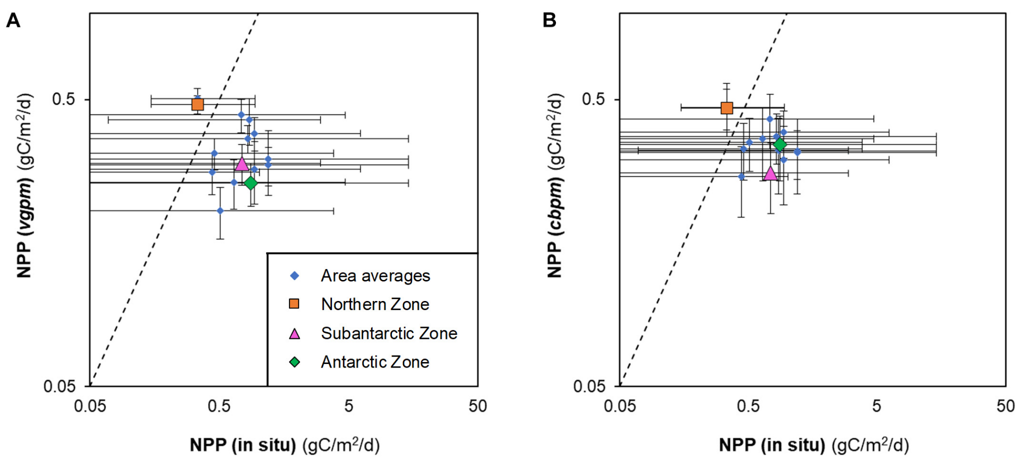

FIGURE 1 | Depth-integrated, net primary productivity (NPP) in the Southern Ocean measured *in situ* from research vessels and estimated from satellite data: **(A)** Vertically Generalised Production Model (*vgpm*); and **(B)** Carbon Based Production Model (*cbpm*). Data are combined as MEASO areas (blue) and zones (orange, pink, green). Dashed lines indicate 1:1 correspondence.

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 ± 15 % (mean ± 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 Subantractic 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 mg m^{-3} y^{-1}, whereas the trends in chl-a were up to ∼0.01 mg m^{-3} 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).

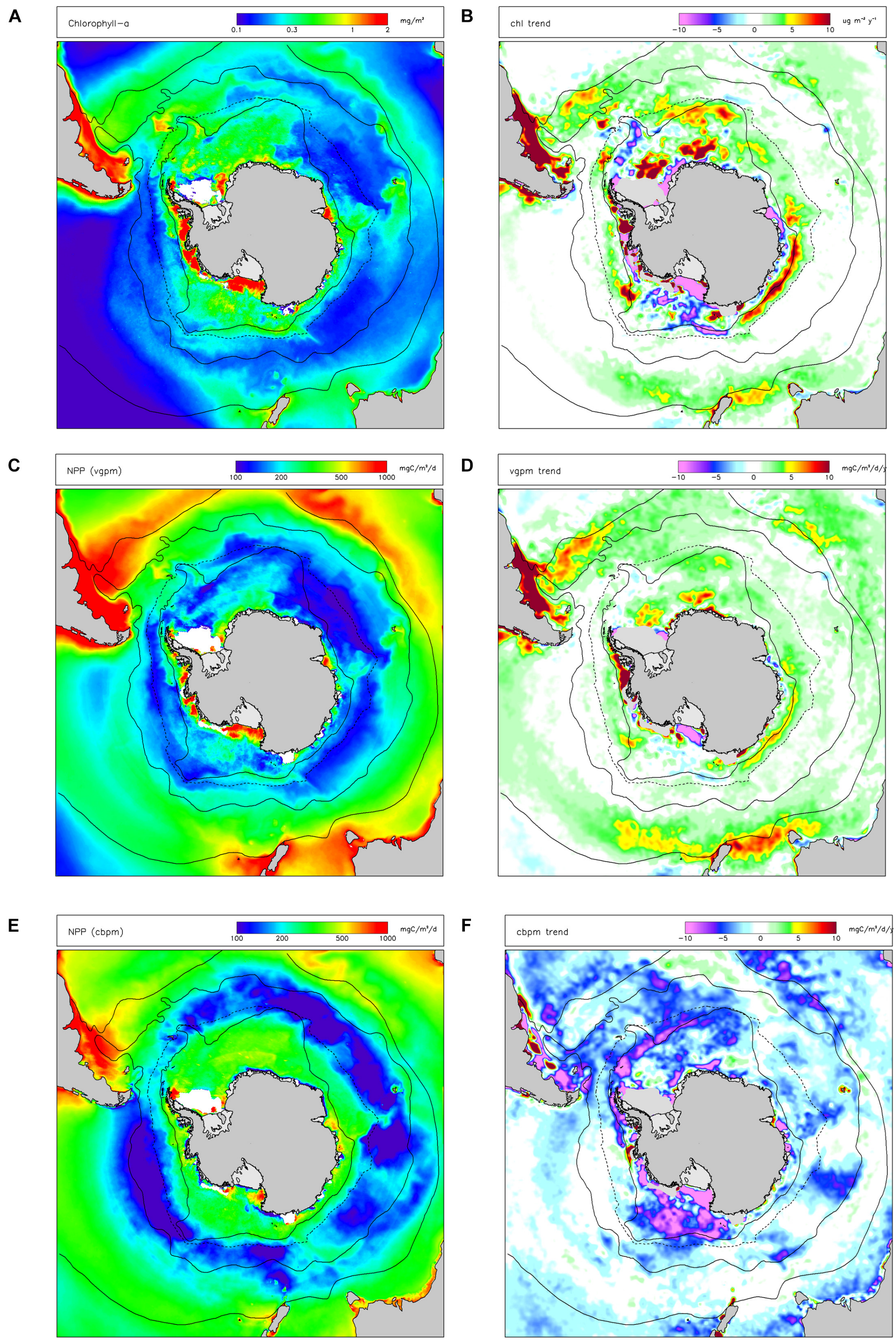

FIGURE 2 | Long-term (1997-2019) mean values of indicators for primary production: **(A)** chlorophyll-a concentration (*chl*); **(C)** net primary production in the water column estimated by the VGPM algorithm (*vgpm*) and the CBPM algorithm (*cbpm*) **(E)**. Linear trends (Sen slopes) over the same 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).

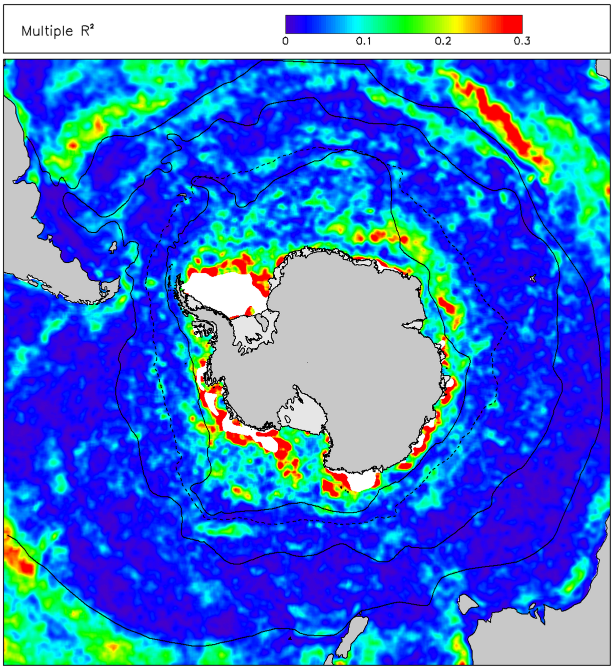

FIGURE 3 | Proportion of variance explained (R^2) in anomalies of chlorophyll-a concentration (*chl*) by a multiple linear regression of anomalies of environmental drivers: sea-surface temperature (*sst*), sea ice concentration (*sea-ice*), mixed layer depth (*mld*) and incident irradiance at the sea-surface (*par*). Other information as **Figure 2**.

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 % y^{-1} ($p < 0.0001$) compared to 0.5 % y^{-1} for *chl* ($p = 0.002$), whereas the overall Southern Ocean trend in *cbpm* was negative (−0.5 % 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 % y^{-1} in magnitude). At the scale of the Southern Ocean, the Sen slope in E_{DCM} was highly significant −3.2 % 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 pCO_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.

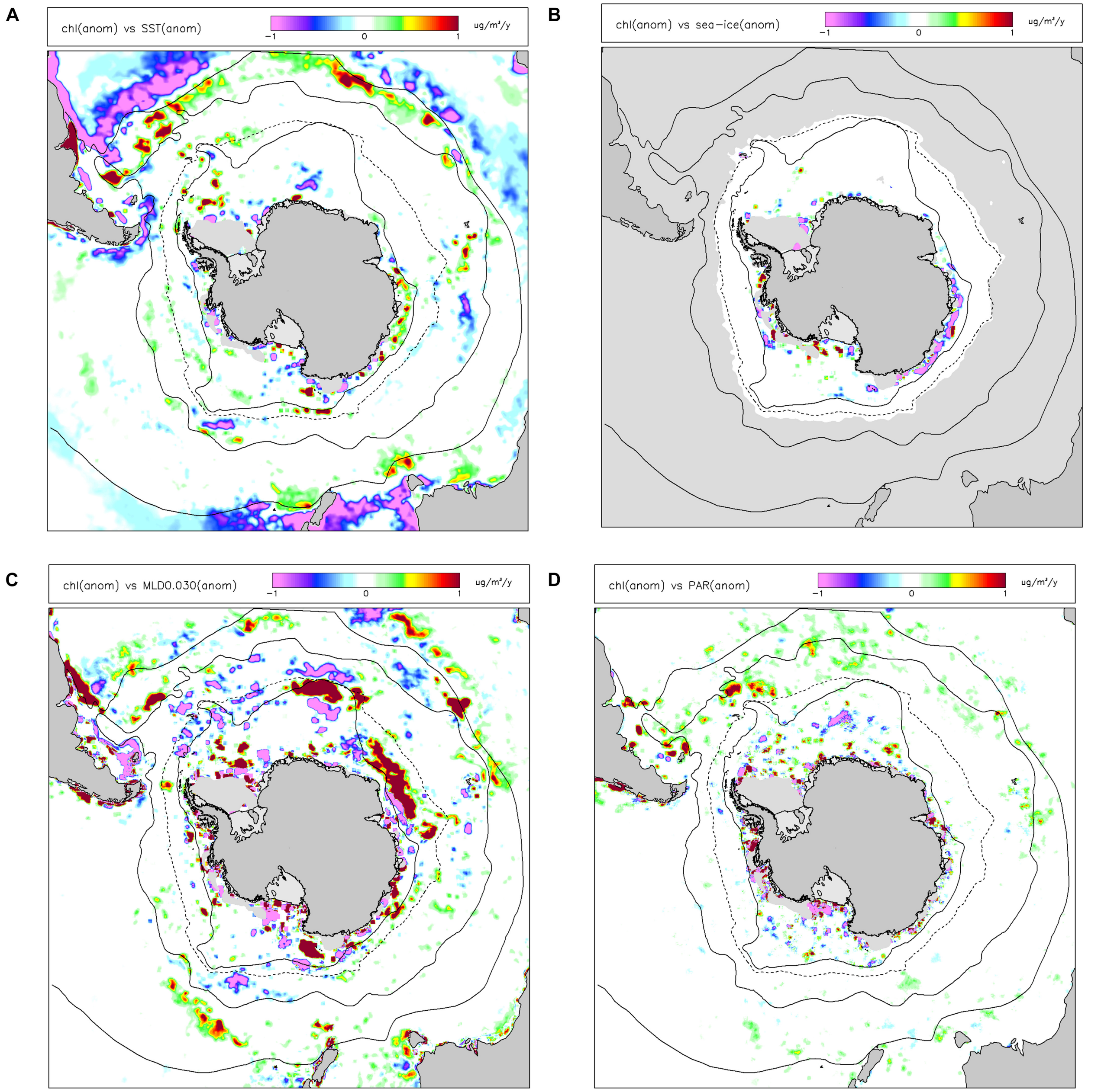

FIGURE 4 | Contribution to linear trends in chlorophyll-a concentration (*chl*) by environmental drivers: **(A)** sea-surface temperature (*sst*); **(B)** sea ice concentration (*sea-ice*); **(C)** mixed layer depth (*mld*); and **(D)** incident irradiance at the sea-surface (*par*). Other information as **Figure 2**.

(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

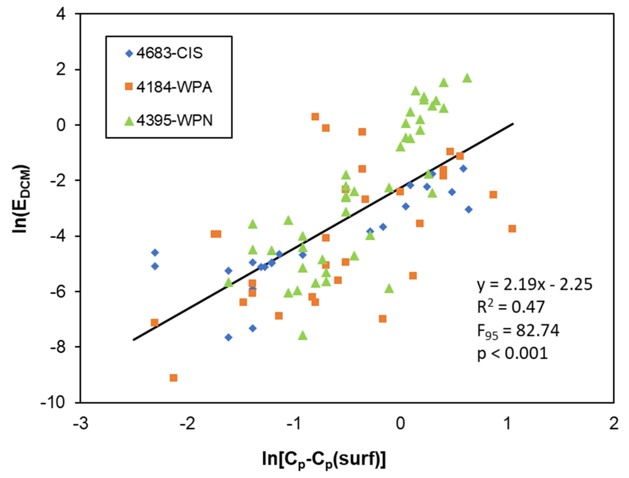

FIGURE 5 | Comparison in log-space between E_{DCM} (irradiance at the base of the mixed layer as Equation 2) and a measure of phytoplankton carbon biomass in the deep chlorophyll maximum (DCM) from profiling floats (C_p-C_p(surf): see text for details).

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., Rousseaux 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

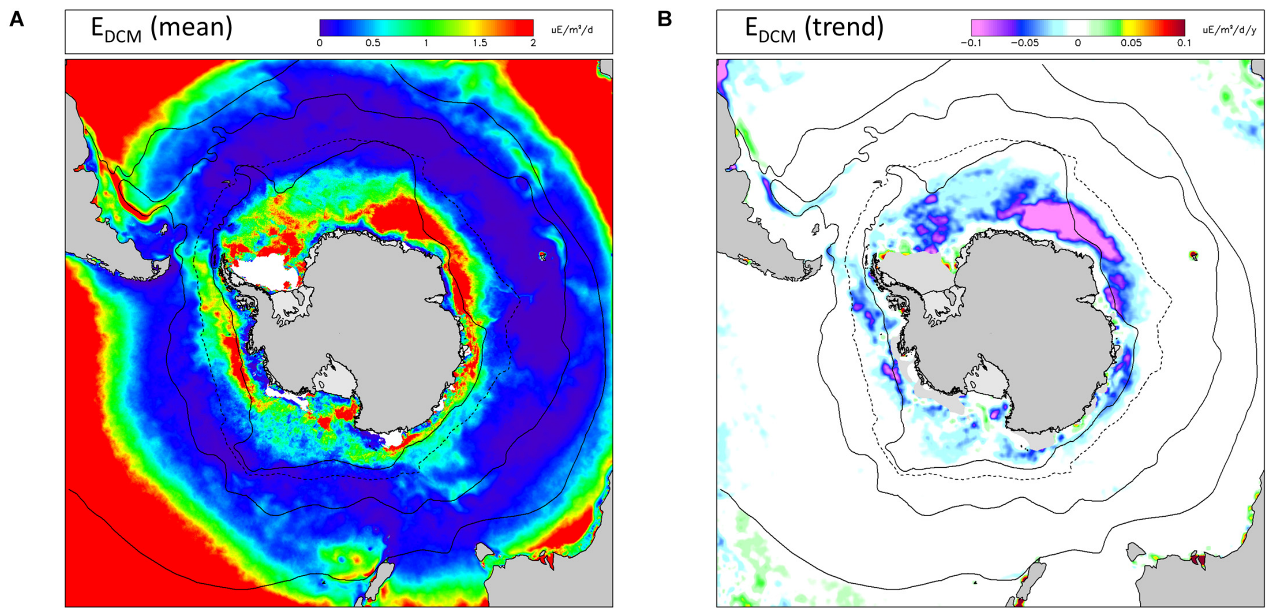

FIGURE 6 | Irradiance at the base of the mixed layer (E_{DCM}) as a proxy for potential primary production in the deep chlorophyll maximum (DCM). **(A)** long-term (1997-2019) mean values; **(B)** linear trends (Sen slopes) over the same period. Other information as **Figure 2**.

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 CMPI5 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) floats[1] 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 heterogenous 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% y^{-1}; ↗ significant increasing trend < 1% y^{-1}; – no significant trend over the period analysed; ↘ significant decreasing trend < 1% y^{-1}; ↓ significant decreasing trend > 1% 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.*

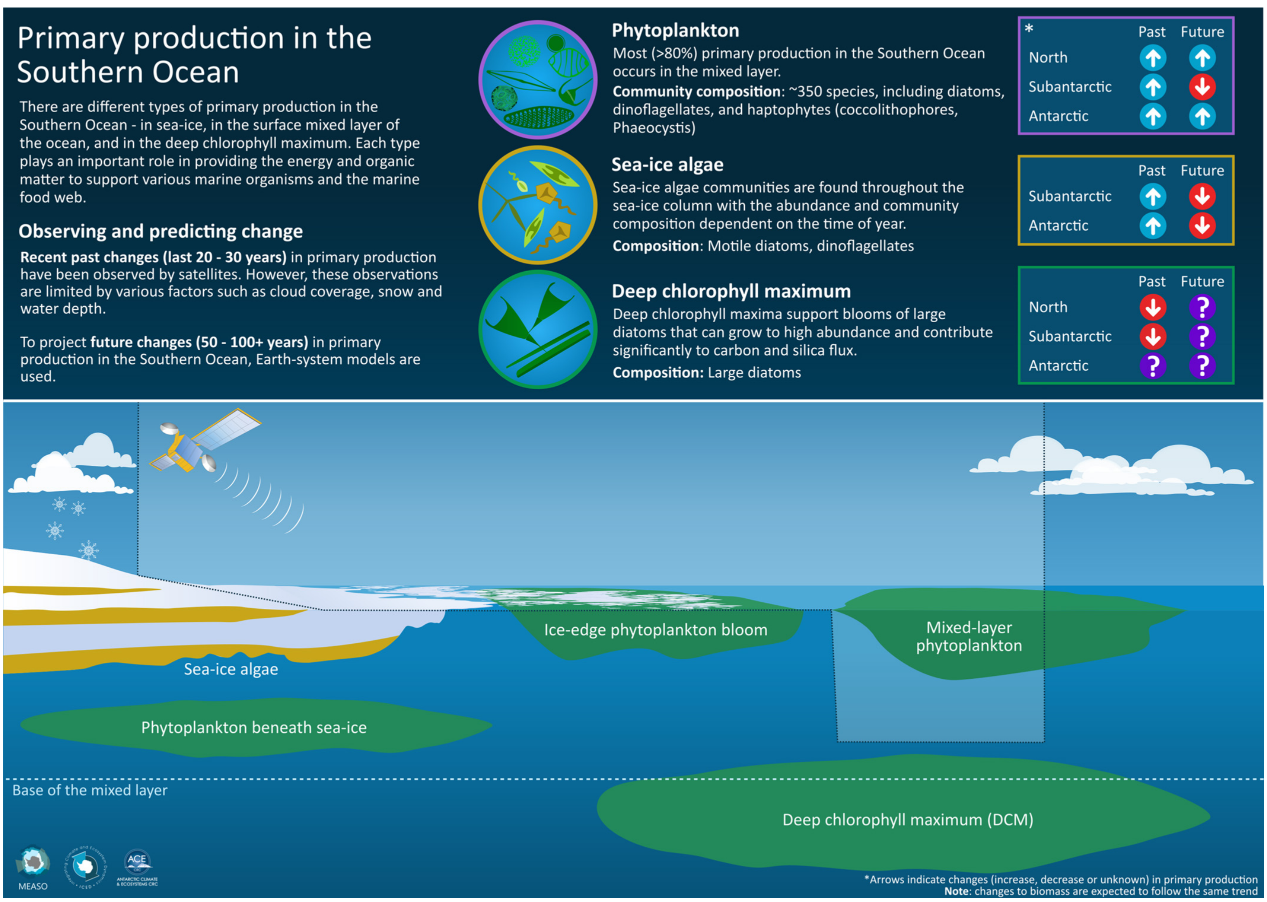

FIGURE 7 | There are different types of primary production in the Southern Ocean – in sea ice, in the surface mixed-layer of the ocean, and in the deep chlorophyll maximum (DCM). Only some of these types of primary production can be observed by satellite over the last 20–30 years. Earth-system models 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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The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.592027/full#supplementary-material

REFERENCES

Alvain, S., and d'Ovidio, F. (2014). "Phytoplankton diversity in the Southern Ocean: a satellite view. Chapter 6.2," in *Biogeographic Atlas of the Southern Ocean*, eds C. De Broyer, P. Koubbi, H. J. Griffiths, B. Raymond, C. Udekem d'Acoz, A. P. Van de Putte, et al. (Cambridge: Scientific Committee on Antarctic Research), 260–265.

Andrew, S. M., Morell, H. T., Strzepek, R. F., Boyd, P. W., and Ellwood, M. J. (2019). Iron availability influences the tolerance of Southern Ocean phytoplankton to warming and elevated irradiance. *Front. Mar. Sci.* 6:681. doi: 10.3389/fmars.2019.00681

Aracena, C., González, H. E., Garcés-Vargas, J., Lange, C. B., Pantoja, S., Muñoz, F., et al. (2018). Primary production in the Southern Ocean, 1997–2006. *J. Geophys. Res. Oceans* 113:C08004. doi: 10.1029/2007JC004551

Arrigo, K., Sullivan, C., and Kremer, J. (1991). A bio-optical model of Antarctic sea ice. *J. Geophys. Res. Oceans* 96, 581–610.

Arrigo, K., Worthen, D., Lizotte, M., and Dixon, P. (1997). Primary production in Antarctic sea ice. *Science* 276, 394–397. doi: 10.1126/science.276.5311.394

Arrigo, K. R. (2014). Sea Ice Ecosystems. *Ann. Rev. Mar. Sci.* 6, 439–467.

Arrigo, K. R., Mills, M. M., Kropuenske, L. R., van Dijken, G. L., Alderkamp, A. —C., and Robinson, D. H. (2010). Photophysiology in two major Southern Ocean phytoplankton taxa: photosynthesis and growth of *Phaeocystis antarctica* and *Fragilariopsus cylindrus* under different irradiance levels. *Integr. Comp. Biol.* 50, 950–966. doi: 10.1093/icb/icq021

Arrigo, K. R., and Sullivan, C. W. (1994). A high-resolution bio-optical model of microalgal growth: Testing using sea-ice algal community time-series data. *Limnol. Oceanogr.* 39, 609–631. doi: 10.4319/lo.1994.39.3.0609

Arrigo, K. R., van Dijken, G. L., and Bushinsky, S. (2008). Primary production in the Southern Ocean, 1997–2006. *J. Geophys. Res. Oceans* 113:C08004.

Arrigo, K. R., van Dijken, G. L., and Strong, A. L. (2015). Environmental controls of marine productivity hot spots around Antarctica. *J. Geophys. Res. Oceans* 120, 5545–5565. doi: 10.1002/2015JC010888

Arrigo, K. R., Worthen, D. L., Dixon, P., and Lizotte, M. P. (1998). "Primary productivity of near surface communities within Antarctic pack ice," in *Antarctic Sea Ice Biological Processes, Interactions, and Variability: Antarctic Research Series*, Vol. 73, eds M. P. Lizotte and K. R. Arrigo (Washington, DC: American Geophysical Union), 23–43. doi: 10.1029/ar073p0023

Arteaga, L. A., Boss, E., Behrenfeld, M. J., Westberry, T. K., and Sarmiento, J. L. (2020). Seasonal modulation of phytoplankton biomass in the Southern Ocean. *Nat. Commun.* 11:5364. doi: 10.1038/s41467-020-19157-2

Atkinson, A., Siegel, V., Pakhomov, E., and Rothery, P. (2004). Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432, 100–103. doi: 10.1038/nature02996

Balch, W. M., Bates, N. R., Lam, P. J., Twining, B. S., Rosengard, S. Z., Bowler, B. C., et al. (2016). Factors regulating the Great Calcite Belt in the Southern Ocean and its biogeochemical significance. *Glob. Biogeochem. Cycles* 30, 1124–1144. doi: 10.1002/2016gb005414

Balch, W. M., Drapeau, D. T., Bowler, B. C., Lyczskowski, E., Booth, E. S., and Alley, D. (2011). The contribution of coccolithophores to the optical and inorganic carbon budgets during the Southern Ocean Gas Exchange Experiment: new evidence in support of the "Great Calcite Belt" hypothesis. *J. Geophys. Res. Oceans* 116:C00F06. doi: 10.1029/2011JC006941

Banse, K. (1996). Low seasonality of low concentrations of surface chlorophyll in the Subantarctic water ring: under- water irradiance, iron, or grazing? *Prog. Oceanogr.* 37, 241–291. doi: 10.1016/s0079-6611(96)00006-7

Behrenfeld, M. J. (2014). Climate-mediated dance of the plankton. *Nat. Clim. Change* 4, 880–887. doi: 10.1038/nclimate2349

Behrenfeld, M. J., Boss, E., Siegel, D. A., and Shea, D. M. (2005). Carbon-based ocean productivity and phytoplankton physiology from space. *Glob. Biogeochem. Cycles* 19:GB1006.

Behrenfeld, M. J., and Falkowski, P. G. (1997). Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol. Oceanogr.* 42, 1–20. doi: 10.4319/lo.1997.42.1.0001

Biermann, A., Lewandowska, A., Engel, A., and Riebesell, U. (2015). Organic matter partitioning and stoichiometry in response to rising water temperature and copepod grazing. *Mar. Ecol. Prog. Ser.* 522, 49–65. doi: 10.3354/meps11148

Blain, S., Quéguiner, B., Armand, L., Belviso, S., Bombled, B., Bopp, L., et al. (2007). Effect of natural iron fertilization on carbon sequestration in the Southern Ocean. *Nature* 446, 1070–1074.

Boyd, P., and Ellwood, M. (2010). The biogeochemical cycle of iron in the ocean. *Nat. Geosci.* 3, 675–682. doi: 10.1038/ngeo964

Boyd, P. W. (2019). Physiology and iron modulate diverse responses of diatoms to a warming Southern Ocean. *Nat. Clim. Change* 9, 148–152. doi: 10.1038/s41558-018-0389-1

Boyd, P. W., Arrigo, K. R., Strzepek, R., and van Dijken, G. L. (2012). Mapping phytoplankton iron utilization: Insights into Southern Ocean supply mechanisms. *J. Geophys. Res. Oceans* 117:C06009. doi: 10.1029/2011JC007726

Boyd, P. W., and Brown, C. J. (2015). Modes of interaction between environmental drives and marine biota. *Front. Mar. Sci.* 2:9. doi: 10.3389/fmars.2015.00009

Boyd, P. W., Crossley, A. C., DiTullio, G. R., Griffiths, F. B., Hutchins, D. A., Queguiner, B., et al. (2001). Control of phytoplankton growth by iron supply and irradiance in the subantarctic Southern Ocean: experimental results from the SAZ Project. *J. Geophys. Res. Oceans* 106, 31573–31583. doi: 10.1029/2000jc000348

Boyd, P. W., Dillingham, P. W., McGraw, C. M., Armstrong, E. A., Cornwall, C. E., Feng, Y.-Y., et al. (2016). Physiological responses of a Southern Ocean diatom to complex future ocean conditions. *Nat. Clim. Change* 6, 207–213. doi: 10.1038/nclimate2811

Boyd, P. W., Kawaguchi, S., Strzepek, R., Meiners, K., Hallegraeff, G., McMinn, A., et al. (2019). *Report Card: Potential Tipping Points for Life in the Southern Ocean*. Hobart, TAS: Antarctic Climate and Ecosystems Cooperative Research Centre, doi: 10.25959/100.00031768

Boyd, P. W., Lennartz, S. T., Glover, D. M., and Doney, S. C. (2014). Biological ramifications of climate-change mediated oceanic multi-stressors. *Nat. Clim. Change* 5, 71–79. doi: 10.1038/NCLIMATE2441

Boyer, T. P., Antonov, J. I., Baranova, O. K., Coleman, C., Garcia, H. E., Grodsky, A., et al. (2013). "World Ocean database 2013," in *NOAA Atlas NESDIS*, Vol. 72, ed. S. Levitus (Silver Spring, MD: NOAA), 209.

Bracher, A. U., Kroon, B. M. A., and Lucas, M. I. (1999). Primary production, physiological state and composition of phytoplankton in the Atlantic sector of the Southern Ocean. *Mar. Ecol. Prog. Ser.* 190, 1–16. doi: 10.3354/meps190001

Briggs, E. M., Martz, T. R., Talley, L. D., Mazloff, M. R., and Johnson, K. S. (2018). Physical and biological drivers of biogeochemical tracers within the seasonal sea ice zone of the Southern Ocean from profiling floats. *J. Geophys. Res. Oceans* 123, 746–758. doi: 10.1002/2017jc012846

Brown, M. S., Munro, D. R., Feehan, C. J., Sweeney, C., Ducklow, H. W., and Schofield, O. M. (2019). Enhanced oceanic CO2 uptake along the rapidly changing West Antarctic Peninsula. *Nat. Clim. Change* 9, 678–683. doi: 10.1038/s41558-41019-40552-41553

Buongiorno Nardelli, B., Guinehut, S., Verbrugge, N., Cotroneo, Y., Zambianchi, E., and Iudicone, D. (2017). Southern Ocean mixed-layer seasonal and interannual variations from combined satellite and in situ data. *J. Geophys. Res. Oceans* 122, 10042–10060. doi: 10.1002/2017JC013314

Cadée, G., González, H., and Schnack-Schiel, S. (1992). Krill diet affects faecal string settling. *Polar Biol.* 12, 75–80. doi: 10.1007/978-3-642-77595-6

Cael, B. B., and Follows, M. J. (2016). On the temperature dependence of oceanic export efficiency. *Geophys. Res. Lett.* 43, 5170–5175. doi: 10.1002/2016GL068877

Campbell, J. W., and Aarup, T. (1989). Photosynthetically available radiation at high latitudes. *Limnol. Oceanogr.* 34, 1490–1499. doi: 10.4319/lo.1989.34.8.1490

Caron, D. A., and Hutchins, D. A. (2013). The effects of changing climate on microzooplankton grazing and community structure: drivers, predictions and knowledge gaps. *J. Plank. Res.* 35, 235–252. doi: 10.1093/plankt/fbs091

Carranza, M. M., Gille, S. T., Franks, P. J., Johnson, K. S., Pinkel, R., and Girton, J. B. (2018). When mixed layers are not mixed. Storm-driven mixing and bio-optical vertical gradients in mixed layers of the Southern Ocean. *J. Geophys. Res. Oceans* 123, 7264–7289. doi: 10.1029/2018jc014416

Cassar, N., Bender, M. L., Barnett, B. A., Fan, S., Moxim, W. J., Levy, H., et al. (2007). The Southern Ocean biological response to Aeolian iron deposition. *Science* 317, 1067–1070. doi: 10.1126/science.1144602

Cavalieri, D., Gloerson, P., and Zwally, J. (1990). "DMSP SSM/I daily polar gridded sea-ice concentrations, 1997 to 2006," in *Digital media*, eds J. Maslanik and J. Stroeve (Boulder, CO: National Snow and Ice Data Center).

Chassignet, E. P., Hurlburt, H. E., Smedstad, O. M., Halliwell, G. R., Hogan, P. J., Wallcraft, A. J., et al. (2007). The HYCOM (HYbrid Coordinate Ocean Model) data assimilative system. *J. Mar. Syst.* 65, 60–83.

Clark, D. K. (1997). *MODIS Algorithm Theoretical Basis Document – Bio-optical algorithms – Case I waters*. Washington, DC: NASA.

Cullen, J. J. (2015). Subsurface chlorophyll maximum layers: Enduring enigma or mystery solved? *Ann. Rev. Mar. Sci.* 7, 207–239. doi: 10.1146/annurev-marine-010213-135111

Daly, K. (1990). Overwintering development, growth, and feeding of larval Euphausia superba in the Antarctic marginal ice zone. *Limnol. Oceanogr.* 35, 1564–1576. doi: 10.4319/lo.1990.35.7.1564

de Baar, H. J. W., de Jong, J. T. M., Bakker, D. C. E., Löscher, B. M., Veth, C., Bathmann, U., et al. (1995). Importance of iron for plankton blooms and carbon dioxide drawdown in the Southern Ocean. *Nature* 373, 412–415. doi: 10.1038/373412a0

Del Castillo, C. E., Signorini, S. R., Karaköylü, E. M., and Rivero—Calle, S. (2019). Is the Southern Ocean getting greener? *Geophys. Res. Lett.* 46, 6034–6040. doi: 10.1029/2019gl083163

Deppeler, S. L., and Davidson, A. T. (2017). Southern Ocean phytoplankton in a changing climate. *Front. Mar. Sci.* 4:40. doi: 10.3389/fmars.2017.00040

Dierssen, H. M., Vernet, M., and Smith, R. C. (2000). Optimizing models for remotely estimating primary production in Antarctic coastal waters. *Antarct. Sci.* 12, 20–32. doi: 10.1017/S0954102000000043

Doblin, M. A., Petrou, K. L., Shelly, K., Westwood, K., van den Enden, R., Wright, S., et al. (2011). Diel variation of chlorophyll-a fluorescence, phytoplankton pigments and productivity in the Sub-Antarctic and Polar Front Zones south of Tasmania, Australia. *Deep-Sea Res. II* 58, 2189–2199. doi: 10.1016/j.dsr2.2011.05.021

Doney, S. C. (2006). Oceanography – Plankton in a warmer world. *Nature* 444, 695–696. doi: 10.1038/444695a

El-Sayed, S. Z. (1970). "On the productivity of the Southern Ocean," in *Antarctic Ecology*, Vol. I, ed. M. W. Holdgate (New York: Academic Press), 119–135.

El-Sayed, S. Z., Holm-Hansen, O., and Biggs, D. C. (1983). Phytoplankton standing crop, primary productivity, and near-surface nitrogenous nutrient fields in the Ross Sea, Antarctica. *Deep Sea Res. I* 30, 871–886. doi: 10.1016/0198-0149(83)90005-5

El-Sayed, S. Z., and Mandelli, E. F. (1965). "Primary production and standing crop of phytoplankton in the Weddell Sea and Drake Passage," in *Biology of the Antarctic Sea II*, Vol. 5, ed. G. A. Llano (Washington, DC: American Geophysical Union), 87–106. doi: 10.1029/ar005p0087

El-Sayed, S. Z., and Taguchi, S. (1981). Primary production and standing crop of phytoplankton along the ice-edge in theWeddell Sea. *Deep Sea Res. I* 28, 1017–1032. doi: 10.1016/0198-0149(81)90015-7

Figueiras, F. G., Estrada, M., Lopez, O., and Arbones, B. (1998). Photosynthetic parameters and primary production in the Bransfield Strait: relationships with mesoscale hydrographic structures. *J. Mar. Syst.* 17, 129–141. doi: 10.1016/s0924-7963(98)00034-7

Finkel, Z. V., Beardall, J., Flynn, K. J., Quigg, A., Rees, T. A. V., and Raven, J. A. (2010). Phytoplankton in a changing world: cell size and elemental stoichiometry. *J. Plank. Res.* 32, 119–137. doi: 10.1093/plankt/fbp098

Freeman, N. M., Munro, D. R., Sprintall, J., Mazloff, M. R., Purkey, S. G., Rosso, I., et al. (2019). The observed seasonal cycle of macronutrients in Drake Passage: relationship to fronts and utility as a model metric. *J. Geophys. Res. Oceans* 124, 4763–4783. doi: 10.1029/2019jc015052

Frouin, R., McPherson, J., Ueyoshi, K., and Franz, B. A. (2012). A time series of photosynthetically available radiation at the ocean surface from SeaWiFS and MODIS data. *Rem. Sens. Mar. Environ.* II:852519. doi: 10.1117/12.981264

Garibotti, I., Vernet, M., Smith, R. C., and Ferrario, M. E. (2005). Interannual variability in the distribution of the phytoplankton standing stock across the seasonal sea-ice zone west of the Antarctic Peninsula. *J. Plankton Res.* 27, 825–843. doi: 10.1093/plankt/fbi056

Grossi, S. M., Kottmeier, S. T., Moe, R. L., Taylor, G. T., and Sullivan, C. W. (1987). Sea ice microbial communities. VI. Growth and. primary production in bottom ice under graded snow cover. *Mar. Ecol. Prog. Ser.* 35, 153–164. doi: 10.3354/meps035153

Guglielmo, L., Granata, A., and Greco, S. (1998). Distribution and abundance of postlarval and juvenile Pleuragramma antarcticum (Pisces, Nototheniidae) off Terra Nova Bay (Ross Seas Antarctica). *Polar Biol.* 19, 37–51. doi: 10.1007/s003000050214

Haentjens, N., Boss, E., and Talley, L. D. (2017). Revisiting Ocean Color algorithms for chlorophyll a and particulate organic carbon in the Southern Ocean using biogeochemical floats. *J. Geophys. Res. Oceans* 122, 6583–6593. doi: 10.1002/2017JC012844

Hauck, J., Völker, C., Wolf-Gladrow, D. A., Laufkötter, C., Vogt, M., Aumont, O., et al. (2015). On the Southern Ocean CO2 uptake and the role of the biological carbon pump in the 21st century. *Global Biogeochem. Cycles* 29, 1451–1470. doi: 10.1002/2015GB005140

Helbling, E. W., Villafañe, V. E., and Holm-Hansen, O. (1995). Variability of phytoplankton distribution and primary production around Elephant Island, Antarctica, during 1990–1993. *Polar Biol.* 15, 233–246.

Henley, S., Cavan, E. L., Fawcett, S. E., Kerr, R., Monteiro, T., Sherrell, R. M., et al. (2020). Changing biogeochemistry of the Southern Ocean and its ecosystem implications. *Front. Mar. Sci.* 7:581. doi: 10.3389/fmars.2020.00581

Henson, S., Le Moigne, F., and Giering, S. (2019). Drivers of carbon export efficiency in the global ocean. *Glob. Biogeochem. Cycles* 33, 891–903. doi: 10.1029/2018GB006158

Henson, S. E., Sarmiento, J. L., Dunne, J. P., Bopp, L., Lima, L., Doney, S. C., et al. (2010). Detection of anthropogenic climate change in satellite records of ocean chlorophyll and productivity. *Biogeoscience* 7, 621–640. doi: 10.5194/bg-7-621-2010

Hill, S. L., Murphy, E. J., Reid, K., Trathan, P. N., and Constable, A. J. (2006). Modelling Southern Ocean ecosystems: krill, the food-web, and the impacts of harvesting. *Biol. Rev.* 81, 581–608. doi: 10.1017/S1464793106007123

Hipel, K. W., and McLeod, A. I. (1994). *Time Series Modelling of Water Resources and Environmental Systems*. Amsterdam: Elsevier.

Hiscock, M. R., Marra, J., Smith, W. O. J., Goericke, R., Measures, C., Vink, S., et al. (2003). Primary productivity and its regulation in the Pacific Sector of the Southern Ocean. *Deep Sea Res. II* 50, 533–558. doi: 10.1016/S0967-0645(02)00583-0

Hixson, S. M., and Arts, M. T. (2016). Climate warming is predicted to reduce omega-3, long-chain, polyunsaturated fatty acid production in phytoplankton. *Glob. Change Biol.* 22, 2744–2755. doi: 10.1111/gcb.13295

Hobbs, W. R., Massom, R., Stammerjohn, S., Reid, P., Williams, G., and Meier, W. (2016). A review of recent changes in Southern Ocean sea ice, their drivers and forcings. *Glob. Planet Change* 143, 228–250. doi: 10.1016/j.gloplacha.2016.06.008

Höfer, J., Giesecke, R., Hopwood, M. J., Carrera, V., Alarcón, E., and González, H. E. (2019). The role of water column stability and wind mixing in the production/export dynamics of two bays in the Western Antarctic Peninsula. *Prog. Oceanogr.* 174, 105–116. doi: 10.1016/j.pocean.2019.01.005

Holm-Hansen, O., and Mitchell, B. G. (1991). Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region. *Deep Sea Res.* 38, 961–980. doi: 10.1016/0198-0149(91)90092-t

Hoppe, C. J. M., Hassler, C. S., Payne, C. D., Tortell, P. D., Rost, B., and Trimborn, S. (2013). Iron limitation modulates Ocean Acidification effects on Southern Ocean phytoplankton communities. *PLoS One* 8:e79890. doi: 10.1371/journal.pone.0079890

Hoppe, C. J. M., Klaas, C., Ossebaar, S., Soppa, M. A., Cheah, W., Laglera, L. M., et al. (2017). Controls of primary production in two phytoplankton blooms in the Antarctic Circumpolar Current. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 138, 63–73. doi: 10.1016/j.dsr2.2015.10.005

Hopwood, M. J., Carroll, D., Höfer, J., Achterberg, E. P., Meire, L., Le Moigne, F. A. C., et al. (2019). Highly variable iron content modulates iceberg-ocean fertilisation and potential carbon export. *Nat. Commun.* 10:5261. doi: 10.1038/s41467-019-13231-0

Horne, A. J., Fogg, G. E., and Eagle, D. J. (1969). Studies in situ of the primary production of an area of inshore Antarctic Sea. *J. Mar. Biol. Ass. UK.* 49, 393–405. doi: 10.1017/s0025315400035980

Hutchins, D. A., and Boyd, P. W. (2016). Marine phytoplankton and the changing ocean iron cycle. *Nat. Clim. Change* 6, 1072–1079. doi: 10.1038/nclimate3147

IPCC (2019). "Summary for Policymakers," in *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*, eds H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, et al. (Geneva: IPCC).

Jena, B. (2017). The effect of phytoplankton pigment composition and packaging on the retrieval of chlorophyll-a concentration from satellite observations in the Southern Ocean. *Int. J. Rem. Sens.* 38, 3763–3784. doi: 10.1080/01431161.2017.1308034

Johnson, R., Strutton, P. G., Wright, S. W., McMinn, A., and Meiners, K. M. (2013). Three improved Satellite Chlorophyll algorithms for the Southern Ocean. *J. Geophys. Res. Oceans* 118, 3694–3703. doi: 10.1002/jgrc.20270

Karl, D. M., Tilbrook, B. D., and Tien, G. (1991). Seasonal coupling of organic matter production and particle flux in the western Bransfield Strait, Antartica. *Deep Sea Res. I* 38, 1097–1126. doi: 10.1016/0198-0149(91)90098-z

Kaufman, D. E., Friedrichs, M. A. M., Smith, W. O. Jr., Hofmann, E. E., Dinniman, M. S., and Hemmings, J. C. P. (2017). Climate change impacts on southern Ross Sea phytoplankton composition, productivity, and export. *J. Geophys. Res. Oceans* 122, 2339–2359. doi: 10.1002/2016jc012514

Kemp, A. E. S., Pearce, R. B., Grigorov, I., Rance, J., Lange, C. B., Quilty, P., et al. (2006). Production of giant marine diatoms and their export at oceanic frontal zones: implications for Si and C flux from stratified oceans. *Glob. Biogeochem. Cycles* 20, 1–13. doi: 10.1029/2006GB002698

Kendall, M. G. (1975). *Rank Correlation Methods*. London: Griffin.

Kim, H., Ducklow, H. W., Abele, D., Ruiz Barlett, E. M., Buma, A. G. J., Meredith, M. P., et al. (2018). Inter-decadal variability of phytoplankton biomass along the coastal West Antarctic Peninsula. *Philos. T. R. Soc. A* 376:20170179. doi: 10.1098/rsta.2017.0179

Kohlbach, D., Lange, B. A., Schaafsma, F. L., David, C., Vortkamp, M., Graeve, M., et al. (2017). Ice algae-produced carbon is critical for overwintering of Antarctic Krill *Euphausia superba*. *Front. Mar. Sci.* 4:310. doi: 10.3389/fmars.2017.00310

Kostov, Y., Marshall, J., Hausmann, U., Armour, K. C., Ferreira, D., Holland, M., et al. (2016). Fast and slow responses of Southern Ocean sea surface temperature to SAM in coupled climate models. *Clim. Dyn.* 48, 1595–1609. doi: 10.1007/s00382-016-3162-z

Kottmeier, S. T., Grossi, S. M., and Sullivan, C. W. (1987). Sea ice microbial communities. VIII. Bacterial production in annual sea ice of McMurdo Sound, Antarctica. *Mar. Ecol. Prog. Ser.* 35, 175–186. doi: 10.3354/meps035175

Kottmeier, S. T., and Sullivan, C. W. (1990). Bacterial biomass and production in pack ice of Antarctic marginal ice edge zones. *Deep Sea Res. I* 37, 1311–1330. doi: 10.1016/0198-0149(90)90045-w

Kropuenske, L. R., Mills, M. M., Van Dijken, G. L., Alderkamp, A. −C., Berg, G. M., Robinson, D. H., et al. (2010). Strategies and rates of photoacclimation in two major Southern Ocean phytoplankton taxa: *Phaeocystis antarctica* (Haptophyta) and Fragilariopsis cylindrus (Bacillariophyceae). *J. Phycol.* 50, 950–966. doi: 10.1093/icb/icq021

Lannuzel, D., Vancoppenolle, M., van der Merwe, P., de Jong, J., Meiners, K. M., Grotti, M., et al. (2016). Iron in sea ice: review and new insights. *Elementa* 4:000130.

Le Quéré, C., Buitenhuis, E. T., Moriarty, R., Alvain, S., Aumont, O., Bopp, L., et al. (2016). Role of zooplankton dynamics for Southern Ocean phytoplankton biomass and global biogeochemical cycles. *Biogeosciences* 13, 4111–4133. doi: 10.5194/bg-13-4111-2016

Le Quéré, C., Harrison, S. P., Prentice, I. C., Buitenhuis, E. T., Aumont, O., Bopp, L., et al. (2005). Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Glob. Change Biol.* 11, 2016–2040.

Leung, S., Cabré, A., and Marinov, I. (2015). A latitudinally banded phytoplankton response to 21st century climate change in the Southern Ocean across the CMIP5 model suite. *Biogeosciences* 12, 5715–5734. doi: 10.5194/bg-12-5715-2015

Llort, J., Lévy, M., Sallée, J. B., and Tagliabue, A. (2019). Nonmonotonic response of primary production and export to changes in mixed−layer depth in the Southern Ocean. *Geophys. Res. Lett.* 46, 3368–3377. doi: 10.1029/2018GL081788

Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W., et al. (1997). Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387, 897–900. doi: 10.1038/43174

Luxem, K. E., Ellwood, M. J., and Strzepek, R. F. (2017). Intraspecific variability in Phaeocystis antarctica's response to iron and light stress. *PLoS One* 12:e0179751. doi: 10.1371/journal.pone.0179751

Maheshwari, M., Singh, R. K., Oza, S. R., and Kumar, R. (2013). An investigation of the Southern Ocean surface temperature variability using long-term optimum interpolation SST data. *ISRN Oceanogr.* 2013:392632.

Mandelli, E. F., and Burkholder, P. R. (1965). Primary productivity in the Gerlache and Bransfield Straits of Antactica. *J. Mar. Res.* 24, 15–27.

Mann, H. B. (1945). Nonparametric tests against trend. *Econometrica* 13, 245–259. doi: 10.2307/1907187

McKinley, G. A., Fay, A. R., Lovenduski, N. S., and Pilcher, D. J. (2017). Natural variability and anthropogenic trends in the ocean carbon sink. *Ann. Rev. Mar. Sci.* 9, 125–150.

McMinn, A. (2017). Reviews and syntheses: ice acidification, the effects of ocean acidification on sea ice microbial communities. *Biogeosciences* 14, 3927–3935. doi: 10.5194/bg-14-3927-2017

Meiners, K. M., Vancoppenolle, M., Thanassekos, S., Dieckmann, G. S., Thomas, D. N., Tison, J. L., et al. (2012). Chlorophyll a in Antarctic sea ice from historical ice core data. *Geophys. Res. Lett.* 39:L21602. doi: 10.1029/2012GL053478

Meredith, M., Sommerkorn, M., Cassotta, S., Mackintosh, A., Ottersen, G., Derksen, C., et al. (2019). "Polar regions," in *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*, eds H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, et al. (Geneva: IPCC).

Meskhidze, N., and Nenes, A. (2006). Phytoplankton and cloudiness in the Southern Ocean. *Science* 314, 1419–1423. doi: 10.1126/science.1131779

Metzger, J., Hurlburt, H., Wallcraft, A., Smedstad, O. M., Kara, B., Shriver, J., et al. (2007). "1/12° Global HYCOM Evaluation and Validation," in *Proceedings of the 11th HYCOM Consortium Meeting 24-26 April 2007*, (Hancock County, MS: Stennis Space Center).

Meyer, B., Freier, U., Grimm, V., Groeneveld, J., Hunt, B. P. V., Kerwath, S., et al. (2017). The winter pack-ice zone provides a sheltered but food-poor habitat for larval Antarctic krill. *Nat. Ecol. Evol.* 1, 1853–1861. doi: 10.1038/s41559-017-0368-3

Mock, T., Otillar, R., Strauss, J., McMullan, M., Paajanen, P., Schmutz, J., et al. (2017). Evolutionary genomics of the cold-adapted diatom *Fragilariopsis cylindrus*. *Nature* 541, 536–540. doi: 10.1038/nature20803

Moline, M. A., Claustre, H., Frazer, T. K., Schofield, O., and Vernet, M. (2004). Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. *Glob. Change Biol.* 10, 1973–1980. doi: 10.1111/j.1365-2486.2004.00825.x

Moline, M. A., and Prézelin, B. B. (1997). High-resolution time-series data for primary production and related parameters at a Palmer LTER coastal site:

implications for modeling carbon fixation in the southern ocean. *Polar Biol.* 17, 39–53. doi: 10.1007/s003000050103

Mongwe, N. P., Vichi, M., and Monteiro, P. M. S. (2018). The seasonal cycle of pCO2 and CO2 fluxes in the Southern Ocean: Diagnosing anomalies in CMIP5 Earth system models. *Biogeosciences* 155, 2851–2872. doi: 10.5194/bg-15-2851-2018

Montes-Hugo, M., Doney, S. C., Ducklow, H. W., Fraser, W., Martinson, D., Stammerjohn, S. E., et al. (2009). Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science* 323, 1470–1473. doi: 10.1126/science.1164533

Montes-Hugo, M. A., Vernet, M., Martinson, D., Smith, R., and Iannuzzi, R. (2008). Variability on phytoplankton size structure in the western Antarctic Peninsula (1997–2006). *Deep Sea Res II* 55, 2106–2117. doi: 10.1016/j.dsr2.2008.04.036

Moore, J. K., Fu, W., Primeau, F., Britten, G. L., Lindsay, K., Long, M., et al. (2018). Sustained climate warming drives declining marine biological productivity. *Science* 359, 1139–1143. doi: 10.1126/science.aao

Moreau, S., Boyd, P. W., and Strutton, P. G. (2020). Remote assessment of the fate of phytoplankton in the Southern Ocean sea-ice zone. *Nat. Commun.* 11:3108. doi: 10.1038/s41467-020-16931-0

Moreau, S., Ferreyra, G. A., Mercier, B., Lemarchand, K., Lionard, M., Roy, S., et al. (2010). Variability of the microbial community in the Western Antarctic Peninsula from late fall to spring during a low-ice cover year. *Polar Biol.* 33, 1599–1614. doi: 10.1007/s00300-010-0806-z

Moreau, S., Mostajir, B., Bélanger, S., Schloss, I. R., Vancoppenolle, M., Demers, S., et al. (2015). Climate change enhances primary production in the western Antarctic Peninsula. *Glob. Change Biol.* 21, 2191–2205. doi: 10.1111/gcb.12878

Morel, A., Huot, Y., Gentili, B., Werdell, P. J., Hooker, S. B., and Franz, B. A. (2007). Examining the consistency of products derived from various ocean color sensors in open ocean (Case 1) waters in the perspective of a multi-sensor approach. *Rem. Sens. Environ.* 111, 69–88. doi: 10.1016/j.rse.2007.03.012

Moutier, W., Thomalla, S. J., Bernard, S., Wind, G., Ryan-Keogh, T. J., and Smith, M. E. (2019). Evaluation of Chlorophyll-a and POC MODIS aqua products in the Southern Ocean. *Rem. Sens.* 11:1793. doi: 10.3390/rs11151793

NASA Goddard Space Flight Center, Ocean Ecology Laboratory, and Ocean Biology Processing Group. (2018a). *SeaWiFS Ocean Color Reprocessing 2018.0*. Available online at: https://oceancolor.gsfc.nasa.gov/reprocessing/r2018/seawifs/ (accessed June, 2020).

NASA Goddard Space Flight Center, Ocean Ecology Laboratory, and Ocean Biology Processing Group. (2018b). *MODIS/Aqua Ocean Color Reprocessing 2018.0*. Available online at: https://oceancolor.gsfc.nasa.gov/reprocessing/r2018/aqua/ (accessed June, 2020).

Newman, L., Heil, P., Trebilco, R., Katsumata, K., Constable, A., van Wijk, E., et al. (2019). Delivering sustained, coordinated, and integrated observations of the Southern Ocean for global impact. *Front. Mar. Sci.* 6:433. doi: 10.3389/fmars.2019.00433

Nissen, C., Vogt, M., Münnich, M., Gruber, N., and Haumann, F. A. (2018). Factors controlling coccolithophore biogeography in the Southern Ocean. *Biogeosciences* 15, 6997–7024. doi: 10.5194/bg-15-6997-2018

Oliver, E. C. J., Burrows, M. T., Donat, M. G., Gupta, A. S., Alexander, L. V., Perkins-Kirkpatrick, S. E., et al. (2019). Projected Marine Heatwaves in the 21st century and the potential for ecological impact. *Front. Mar. Sci.* 6:734. doi: 10.3389/fmars.2019.00734

O'Reilly, J. E., and Sherman, K. (2016). "Chapter 5.1: primary productivity and trends," in *IOC-UNESCO and UNEP (2016). Large Marine Ecosystems: Status and Trends*, (Nairobi: United Nations Environment Programme), 91–99.

Park, J., Kim, J.-H., Kim, H., Kim, B.-K., Bae, D., Jo, Y.-H., et al. (2019). Reconstruction of ocean color data using machine learning techniques in Polar regions: focusing on Cape Hallett, Ross Sea. *Rem. Sens.* 11:1366. doi: 10.3390/rs11111366

Parslow, J. S., Boyd, P. W., Rintoul, S. R., and Griffiths, F. B. (2001). A persistent subsurface chlorophyll maximum in the Interpolar Frontal Zone south of Australia: seasonal progression and implications for phytoplankton-light-nutrient interactions. *J. Geophys. Res. Oceans* 106, 31543–31557. doi: 10.1029/2000JC000322

Pausch, F., Bischof, K., Trimborn, S., and Jesus, B. (2019). Iron and manganese co-limit growth of the Southern Ocean diatom *Chaetoceros debilis*. *PLoS One* 14:e0221959. doi: 10.1371/journal.pone.0221959

Perissinotto, R., and Pakhomov, E. A. (1998). Contribution of salps to carbon flux of marginal ice zone of the Lazarev Sea, Southern Ocean. *Mar. Biol.* 131, 25–32. doi: 10.1007/s002270050292

Petrou, K., Kranz, S. A., Trimborn, S., Hassler, C. S., Ameijeiras, S. B., Sackett, O., et al. (2016). Southern Ocean phytoplankton physiology in a changing climate. *J. Plant Physiol.* 203, 135–150. doi: 10.1016/j.jplph.2016.05.004

Pinkerton, M. H. (2019). *Change in Environmental Conditions of the Southern Ocean Observed by Satellites and Data-assimilating Models to 2019. CCAMLR Document WG-EMM-19/39*. Concarneau: CCAMLR, 22.

Pinkerton, M. H., and Bradford-Grieve, J. M. (2014). Characterizing foodweb structure to identify potential ecosystem effects of fishing in the Ross Sea, Antarctica. *ICES J. Mar. Sci.* 71, 1542–1553. doi: 10.1093/icesjms/fst230

Pollard, R. T., Salter, I., Sanders, R. J., Lucas, M. I., Moore, C. M., Mills, R. A., et al. (2009). Southern Ocean deep-water carbon export enhanced by natural iron fertilization. *Nature* 457, 577–580. doi: 10.1038/nature07716

Quetin, L. B., Ross, R. M., Frazer, T. K., and Haberman, K. L. (1996). "Factors affecting distribution and abundance of zooplankton, with an emphasis on Antarctic krill, *Euphausia superba*," in *Foundations for Ecological Research West of the Antarctic Peninsula: Antarctic Research Series*, Vol. 70, eds R. M. Ross, E. E. Hofmann, and L. B. Quetin (Washington, DC: American Geophysical Union), 357–371. doi: 10.1029/ar070p0357

Rembauville, M., Briggs, N., Ardyna, M., Uitz, J., Catala, P., Penkerc'ch, C., et al. (2017). Plankton assemblage estimated with BGC-Argo floats in the Southern Ocean: implications for seasonal successions and particle export in the mesopelagic. *J. Geophys. Res. Oceans* 122, 8278–8292. doi: 10.1002/2017JC013067

Reynolds, R. W., Rayner, N. A., Smith, T. M., Stokes, D. C., and Wang, W. (2002). An improved in situ and satellite SST analysis for climate. *J. Clim.* 15, 1609–1625. doi: 10.1175/1520-0442(2002)015<1609:aiisas>2.0.co;2

Rickard, G., and Behrens, E. (2016). CMIP5 earth system models with biogeochemistry: a ross sea assessment. *Antarct. Sci.* 28, 327–346. doi: 10.1017/s0954102016000122

Riser, S. C., Swift, D., and Drucker, R. (2018). Profiling floats in SOCCOM: technical capabilities for studying the Southern Ocean. *J. Geophys. Res. Oceans* 123, 4055–4073. doi: 10.1002/2017jc013419

Rousseaux, C. S., and Gregg, W. W. (2015). Recent decadal trends in global phytoplankton composition. *Glob. Biogeochem. Cycles* 29, 1674–1688. doi: 10.1002/2015GB005139

Saenz, B. T., and Arrigo, K. R. (2012). Simulation of a sea ice ecosystem using a hybrid model for slush layer desalination. *J. Geophys. Res. Oceans* 117:C05007. doi: 10.1029/2011JC007544

Saenz, B. T., and Arrigo, K. R. (2014). Annual primary production in Antarctic sea ice during 2005–2006 from a sea ice state estimate. *J. Geophys. Res. Oceans* 119, 3645–3678. doi: 10.1002/2013jc009677

Saggiomo, V., Carrada, G. C., Mangoni, O., Ribera d'Alcalà, M., and Russo, A. (1998). Spatial and temporal variability of size-fractionated biomass and primary production in the Ross Sea (Antarctica) during austral spring and summer. *J. Mar. Syst.* 17, 115–127. doi: 10.1016/s0924-7963(98)00033-5

Saijo, Y., and Kawashima, T. (1964). Primary production in the Antarctic Ocean. *J. Oceanogr. Soc. Japan* 19, 190–196. doi: 10.5928/kaiyou1942.19.190

Sallée, J.-B. (2018). Southern Ocean warming. *Oceanography* 31, 52–62.

Sallée, J.-B., Llort, J., Tagliabue, A., and Lévy, M. (2015). Characterization of distinct bloom phenology regimes in the Southern Ocean. *ICES J. Mar. Sci.* 72, 1985–1998. doi: 10.1093/icesjms/fsv069

Sarmento, H., Montoya, J. M., Vazquez-Dominguez, E., Vaque, D., and Gasol, J. M. (2010). Warming effects on marine microbial food web processes: how far can we go when it comes to predictions? *Philos. Trans. R. Soc. B Biol. Sci.* 365, 2137–2149. doi: 10.1098/rstb.2010.0045

Sarmiento, J. L. (2013). *Ocean Biogeochemical Dynamics*. Princeton, NJ: Princeton University Press.

Savidge, G., Harbour, D., Gilpin, L. C., and Boyd, P. W. (1995). Phytoplankton distributions and production in the Bellingshausen Sea, Austral spring 1992. *Deep Sea Res. II* 42, 1201–1224. doi: 10.1016/0967-0645(95)00062-u

Schloss, I. R., Wasilowska, A., Dumont, D., Almandoz, G. O., Hernando, M. P., Michaud-Tremblay, C. A., et al. (2014). On the phytoplankton bloom in coastal waters of southern King George Island (Antarctica) in January 2010: An exceptional feature? *Limnol. Oceanogr.* 59, 195–210. doi: 10.4319/lo.2014.59.1.0195

Schofield, O., Brown, M., Kohut, J., Nardelli, S., Saba, G., Waite, N., et al. (2017). Changes in the upper ocean mixed layer and phytoplankton productivity along the West Antarctic Peninsula. *Philos. T. R. Soc. A* 376:20170173. doi: 10.1098/rsta.2017.0173

Sen, P. K. (1968). Estimates of the regression coefficient based on Kendall's tau. *J. Am. Stat. Assess.* 63, 1379–1389. doi: 10.1080/01621459.1968.10480934

Siegenthaler, U., and Sarmiento, J. (1993). Atmospheric carbon dioxide and the ocean. *Nature* 365:119.

Smetacek, V., Scharek, R., and Nothig, E.-M. (1990). "Seasonal and regional variation in the pelagial and its relationship to the life cycle of krill," in *Antarctic Ecosystems, Ecological Change and Conservation*, eds K. R. Kerry and G. Hempel (Berlin: Springer), 103–114. doi: 10.1007/978-3-642-84074-6_10

Smith, G. C., Allard, R., Babin, M., Bertino, L., Chevallier, M., Corlett, G., et al. (2019). Polar ocean observations: a critical gap in the observing system and its effect on environmental prediction. *Front. Mar. Sci.* 6:429. doi: 10.3389/fmars.2019.0042

Smith, W. O. Jr., and Nelson, D. M. (1990). Phytoplankton growth and new production in the Weddell Sea MIZ in the austral spring and autumn. *Limnol. Oceanogr.* 35, 809–821. doi: 10.4319/lo.1990.35.4.0809

Steinacher, M., Joos, F., Frölicher, T. L., Bopp, L., Cadule, P., Cocco, V., et al. (2010). Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences* 7, 979–1005. doi: 10.5194/bg-7-979-2010

Strzepek, R. F., Boyd, P. W., and Sunda, W. G. (2019). Photosynthetic adaptation to low iron, light, and temperature in Southern Ocean phytoplankton. *Proc. Natl Acad. Sci. U.S.A.* 116, 4388–4393. doi: 10.1073/pnas.1810886116

Strzepek, R. F., Hunter, K. A., Frew, R. D., Harrison, P. J., and Boyd, P. W. (2012). Iron-light interactions differ in Southern Ocean phytoplankton. *Limnol. Oceanogr.* 57, 1182–1200. doi: 10.4319/lo.2012.57.4.1182

Tagliabue, A., Bopp, L., Dutay, J., Bowie, A. R., Chever, F., Jean-Baptiste, P., et al. (2010). Hydrothermal contribution to the oceanic dissolved iron inventory. *Nat. Geosci* 3, 252–256. doi: 10.1038/ngeo818

Tedesco, L., and Vichi, M. (2014). Sea ice biogeochemistry: a guide for modellers. *PLoS One* 9:e89217. doi: 10.1371/journal.pone.0089217

Tilstone, G. H., Lange, P. K., Misra, A., Brewin, R. J. W., and Cain, T. (2017). Microphytoplankton photosynthesis, primary production and potential export production in the Atlantic Ocean. *Prog. Oceanogr.* 158, 109–129. doi: 10.1016/j.pocean.2017.01.006

Treguer, P. J. (2014). The Southern Ocean silica cycle. *C. R. Geoscience* 346, 279–286. doi: 10.1016/j.crte.2014.07.003

Trimborn, S., Thoms, S., Bischof, K., and Beszteri, S. (2019). Susceptibility of two Southern Ocean phytoplankton key species to iron limitation and high light. *Front. Mar. Sci.* 6:167. doi: 10.3389/fmars.2019.00167

Trimborn, S., Thoms, S., Brenneis, T., Heiden, J., Beszteri, S., and Bischof, K. (2017). Two Southern Ocean diatoms are more sensitive to ocean acidification and changes in irradiance than the prymnesiophyte *Phaeocystis antarctica*. *Physiol. Plant.* 160, 155–170. doi: 10.1111/ppl.12539

Trull, T. W., Passmore, A., Davies, D. M., Smit, T., Berry, K., and Tilbrook, B. (2018). Distribution of planktonic biogenic carbonate organisms in the Southern Ocean south of Australia: a baseline for ocean acidification impact assessment. *Biogeosciences* 15, 31–49. doi: 10.5194/bg-15-31-2018

Uchida, T., Balwada, D., Abernathey, R., Prend, C. J., Boss, E., and Gille, S. T. (2019). Southern Ocean phytoplankton blooms observed by biogeochemical floats. *J. Geophys. Res. Oceans* 124, 7328–7343. doi: 10.1029/2019JC015355

Uitz, J., Claustre, H., Griffiths, F. B., Ras, J., Garcia, N., and Sandroni, V. (2009). A phytoplankton class− specific primary production model applied to the Kerguelen islands region (Southern Ocean). *Deep Sea Res. I* 56, 541–560. doi: 10.1016/j.dsr.2008.11.006

Vacchi, M., La Mesa, M., Dalù, M., and Macdonald, J. (2004). Early life stages in the life cycle of Antarctic silverfish, Pleuragramma antarcticum in Terra Nova Bay, Ross Sea. *Antarc. Sci.* 16, 299–305. doi: 10.1017/s0954102004002135

Van de Poll, W., Lagunas, M., de Vries, T., Visser, R. J. W., and Buma, A. G. J. (2011). Non−photochemical quenching of chlorophyll fluorescence and xanthophyll cycle responses after excess PAR and UVR in Chaetoceros brevis, Phaeocystis antarctica and coastal Antarctic phytoplankton. *Mar. Ecol. Prog. Ser.* 426, 119–131. doi: 10.3354/meps09000

van Leeuwe, M. A., Tedesco, L., Arrigo, K. R., Assmy, P., Campbell, K., Meiners, K. M., et al. (2018). Microalgal community structure and primary production in Arctic and Antarctic sea ice: a synthesis. *Elem. Sci. Anth.* 6:4. doi: 10.1525/elementa.267

Varela, M., Fernandez, E., and Serret, P. (2002). Size-fractionated phytoplankton biomass and primary production in the Gerlache and south Bransfield Straits (Antarctic Peninsula) in Austral summer 1995–1996. *Deep Sea Res. II* 49, 749–768. doi: 10.1016/s0967-0645(01)00122-9

Vaughan, D. G., Comiso, J. C., Allison, I., Carrasco, J., Kaser, G., Kwok, R., et al. (2013). "Observations: cryosphere," in *Climate Change 2013: The Physical Science Basis, Contribution of Working Group I to the Fifth Assessment Report of the IPCC*, eds T. F. Stocker, G.-K. Qin, M. Plattner, M. M. B. Tignor, S. K. Allen, J. Boschung, et al. (Cambridge: Cambridge University Press), 317–382.

Verlencar, X. N., Somasunder, K., and Qasim, S. Z. (1990). Regeneration of nutrients and biological productivity in Antarctic Waters. *Mar. Ecol. Prog. Ser.* 61, 41–59. doi: 10.3354/meps061041

Vernet, M., Martinson, D., Iannuzzi, R., Stammerjohn, S., Kozlowski, W., Sines, K., et al. (2008). Primary production within the sea-ice zone west of the Antarctic Peninsula: I-sea ice, summer mixed layer, and irradiance. *Deep Res. Part II* 55, 2068–2085. doi: 10.1016/j.dsr2.2008.05.021

Vernet, M., Sines, K., Chakos, D., Cefarelli, A., and Ekern, L. (2011). Impacts on phytoplankton dynamics by free-drifting icebergs in the NW Weddell Sea. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 58, 1422–1435. doi: 10.1016/j.dsr2.2010.11.022

von Bodungen, B., Smetacek, V. S., Tilzer, M. M., and Zeitzschel, B. (1986). Primary production and sedimentation during spring in the Antarctic Peninsula region. *Deep Sea Res. I* 33, 177–194. doi: 10.1016/0198-0149(86)90117-2

Wallcraft, A. J., Metzger, E. J., and Carroll, S. N. (2009). *Software Design Description for the HYbrid Coordinate Ocean Model (HYCOM), Version 2.2. US Naval Research Laboratory Report, NRL/MR/7320-09-9166*. Available online at: https://www.hycom.org/hycom/documentation/63-hycom-users-manual-and-guide (accessed June, 2020).

Westberry, T., Behrenfeld, M. J., Siegel, D. A., and Boss, E. (2008). Carbon-based primary productivity modeling with vertically resolved photoacclimation. *Glob. Biogeochem. Cycles* 22:GB2024. doi: 10.1029/2007GB003078

Wright, S. W., van den Enden, R. L., Pearce, I., Davidson, A. T., Scott, F. J., and Westwood, K. J. (2010). Phytoplankton community structure and stocks in the Southern Ocean (30–80E) determined by CHEMTAX analysis of HPLC pigment signatures. *Deep Sea Res. Part II* 57, 758–778. doi: 10.1016/j.dsr2.2009.06.015

Yue, S., and Wang, C. Y. (2004). The Mann-Kendall test modified by effective sample size to detect trend in serially correlated hydrological series. *Water Res. Manag.* 18, 201–218. doi: 10.1023/B:WARM.0000043140.61082.60

Zhang, L., Delworth, T. L., Cooke, W., and Yang, X. (2018). Natural variability of Southern Ocean convection as driver of observed climate trends. *Nat. Clim. Change* 9, 59–65, doi: 10.1038/s41558-018-0350-3

Zhu, Z., Xu, K., Fu, F., Spackeen, J. L., Bronk, D. A., and Hutchins, D. A. (2016). A comparative study of iron and temperature interactive effects on diatoms and Phaeocystis antarctica from the Ross Sea, Antarctica. *Mar. Ecol. Prog. Ser.* 550, 39–51. doi: 10.3354/meps11732

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