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The response of phytoplankton biomass to transient mixing events in the Southern Ocean

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[1] We examine the sensitivity of surface chlorophyll-*a* concentrations (as a proxy for phytoplankton biomass) to short-term, transient Mixed-Layer variability in the High Nutrient-Low Chlorophyll Southern Ocean during the austral summer. To investigate this sensitivity, we use satellite remote sensing data, Ocean reanalyses, and the biogeochemical model NEMO-PISCES. We find an unexpectedly large spatial variability in the nature of the chlorophyll-*a* response to mixing events in both the observations and the model outputs and our results suggest that the degree of iron limitation (relative to light) seems to be instrumental in dictating these patterns. We propose a conceptual model that provides a first order explanation of the regional and seasonal differences in the response of Chlorophyll-*a* anomalies to transient Mixed-Layer-Depth (MLD) variability. Overall, we suggest that it is the relationship between the seasonal MLD and the corresponding light and iron vertical distributions that dictates the degree of light and iron limitation. This balance then governs the sign of the response to phytoplankton biomass to transient mixing events. **Citation:** Fauchereau, N., A. Tagliabue, L. Bopp, and P. M. S. Monteiro (2011), The response of phytoplankton biomass to transient mixing events in the Southern Ocean, *Geophys. Res. Lett.*, 38, L17601, doi:10.1029/2011GL048498.

1. Introduction

[2] The Southern Ocean (SO) is the largest High Nutrient – Low Chlorophyll region in the world Ocean, characterized by the greatest inventory of macro-nutrients, but low average phytoplankton biomass. This has been attributed to the limitation of phytoplankton growth by both light and iron (Fe), as well as Silica for diatoms in the sub-Antarctic zone [e.g., *Boyd et al.*, 1999; *Martin et al.*, 1990a, 1990b]. The SO is predicted to be heavily impacted by climate change, via alterations in surface water stratification [e.g., *Sarmiento et al.*, 2004]. Model simulations have suggested that greater stratification (due to warming and increased freshwater fluxes) may reduce the vertical nutrient supply and hinder phytoplankton growth [e.g., *Bopp et al.*, 2005] potentially

acting as a positive feedback on climate change. Stratification changes depend on the balance between buoyancy and momentum fluxes, acting on both seasonal and sub-seasonal time-scales. The regional differences and time-scales sensitivity of the primary production response to MLD variability has received little attention but are however critical in better assessing potential changes.

[3] The seasonal evolution of phytoplankton biomass in the SO has been typically attributed to changes in the light limitation in the framework of the critical depth hypothesis [*Sverdrup*, 1953] and to the seasonal cycle of Fe availability [e.g., *Boyd et al.*, 1999; *Boyd*, 2002; *Arrigo et al.*, 2008] both largely controlled by the seasonal changes in Mixed Layer (ML). In general, deep winter ML replenish seasonal ML Fe stocks from below the ferricline, but low average ML irradiance results in little phytoplankton growth South of the Subtropical Front (STF) (winter sea ice is also important at higher latitudes [*Arrigo et al.*, 2008]). The winter/spring transition and the associated shoaling of the ML above the critical depth alleviates light limitation and permits phytoplankton to utilise the available stock of Fe. Summertime depletion of the ML Fe inventory and associated onset of Fe limitation leads to declining growth rates, which are outstripped by grazing rates thus terminating the growing season. Autumn-time deepening of the ML supplies Fe and alleviates Fe limitation, but only provides a short window for growth before seasonal light limitation occurs. This results in a sequence of bottom-up factors limiting phytoplankton growth from light to Fe and then back to light over the seasonal cycle [*Boyd et al.*, 1999].

[4] Variability in the stratification/mixing regimes over sub-seasonal time-scales (i.e., from a few days to a few weeks) have been shown to be important in low latitudes oligotrophic regions where phytoplankton responds to additional nutrient inputs associated with transient deepening of the ML [e.g., *Resplandy et al.*, 2009] and/or upwelling events often in the context of mesoscale / sub-mesoscale variability [e.g., *Pasquero et al.*, 2005; *Lévy et al.*, 2009]. Alongside the seasonal trends, it is possible that sub-seasonal variability in buoyancy / momentum balance might be important in modulating the biogeochemical seasonal cycles in the SO. Its consideration could provide insights into the balance between light and iron limitation and its regional and seasonal variability, the proper understanding of which is critical to assess the sensitivity of the system to climate change [*Boyd*, 2002]. In this study, we use satellite remote sensing, an ocean reanalysis product as well as a biogeochemical model to examine the response of phytoplankton to sub-seasonal variability in MLD as mediated by bottom-up controls. We find a large degree of variability in the response

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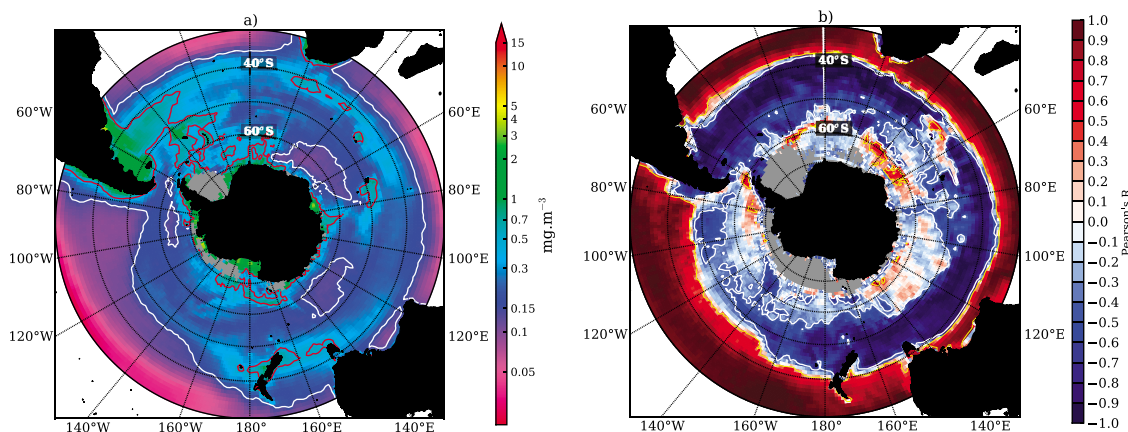


Figure 1. (a) Summer (October–March 1998/99–2009/10) average Chl-a concentrations from GlobColour on a 1 degree grid. Regions where average Chl-a concentrations are above 0.5 mg.m^{-3} (below 0.15 mg.m^{-3}) are contoured in red (white). (b) Correlation coefficients between mean seasonal cycles of Chl-a and MLD, yellow and white contours delineate respectively correlations above 0.4 and below -0.4 . Gray areas indicate where less than 15 weeks are available. Positive correlations at high latitudes (i.e., South of $\sim 50^\circ\text{S}$) do not indicate a Chl-a winter maximum but are related to an early summer bloom (and no estimates available in the core of winter): please refer to text (section 3.1) and Figure S3.

of the phytoplankton biomass to MLD transient anomalies and propose a conceptual model to reconcile these results.

2. Materials and Methods

[5] Chlorophyll-a concentrations (Chl-a) in mg.m^{-3} are obtained from the European Space Agency's GlobColour project at <ftp.acri.fr>. We use Chl-a data for Case I water merged by GlobColour from multiple sensors (SeaWiFS, MERIS, and MODIS-Aqua) using the bio-optical model described by *Maritorena and Siegel* [2005] shown to provide the best fit to in-situ Chl-a for Case I waters. The original 8 days, gridded product at 25 km resolution is interpolated onto a 1 degree \times 1 degree grid. As Chl-a is approximately log-normally distributed [*Campbell*, 1995], the $\log(\text{Chl-a})$ is taken. As in, e.g., *Lévy et al.* [2005, 2007] surface Chl-a is used as a proxy for phytoplankton biomass.

[6] MLDs are taken from the recent Climate Forecast System Reanalysis (CFSR) product. The CFSR is a new high resolution coupled (atmosphere / ocean / land / sea-ice) global National Center for Environmental Prediction (NCEP) Reanalysis for the period 1979–present. The oceanic component is the Modular-Ocean-Model version 4p0d [*Griffies et al.*, 2004] and assimilates XBT (eXpendables Bathy-Termographs) observations as well as temperatures from the ARGO profiling floats. The details of the model components characteristics and assimilation procedure are given by *Saha et al.* [2010]. A validation for the oceanic component is available from *Xue et al.* [2010]: while some large differences exist in the climatology of the MLD compared to observation-based only climatologies, the general improvement in the air-sea heat fluxes, shortwave and longwave radiation and wind-stress [*Xue et al.*, 2010] suggests that the variability in the MLD can be used to the extent that it reflects integration of the variability in the atmospheric forcings. Here the low resolution product (1 degree) has been downloaded from (<ftp://nomads.ncdc.noaa.gov/CFSR/>) and averaged over 8 days.

[7] The Ocean General Circulation and Biogeochemistry model NEMO-PISCES simulates the elemental cycles of C,

N, P, Si Fe, and O_2 , as well as two distinct phytoplankton functional types (nanophytoplankton and diatoms), meso and micro zooplankton, and two size classes of particulate organic matter (see *Aumont and Bopp* [2006] for a full description). NEMO-PISCES has been used for a wide range of ocean biogeochemistry studies over recent years [see, e.g., *Bopp et al.*, 2005] including those specifically aimed at the phytoplankton - Fe coupling in the Southern Ocean [*Tagliabue et al.*, 2009]. For this study, we use a simulation forced by NCEP1 atmospheric re-analysis products between 1948–2009 and analyse the 5-days outputs available from 2000 to 2009.

[8] In order to extract transient events (at the sub-seasonal time-scales) we convolve all time-series with a Gaussian kernel of $\sigma = 3$ (5 for the 5 days model outputs) and subtract the corresponding filtered series, assumed to contain both the seasonal, inter-annual and long-term components. More discussion and an example are available in the auxiliary material (Text S1 and Figures S1 and S2).¹

3. Results and Discussion

3.1. Southern Ocean Biomass Distribution and Seasonal Cycle

[9] As expected, and noted elsewhere [e.g., *Moore and Abbott*, 2000; *Arrigo et al.*, 2008], regions of elevated summer biomass (average Chl-a $\geq 0.5 \text{ mg.m}^{-3}$, contoured in red, Figure 1a) are related to known Fe sources, such as shelves and plateaux, Islands and the Marginal Ice Zone. Conversely, low biomass regions (Chl-a $\leq 0.15 \text{ mg.m}^{-3}$, contoured in white) are also evident south of $\sim 50^\circ\text{S}$ and are in sharp contrast with neighbouring high biomass regions. Since they are away from known sources of Fe, associated with relatively deep bathymetry and outside the seasonal ice zone we suggest here that these regions are chronically Fe limited.

[10] The correlation coefficients between the mean seasonal cycles of Chl-a and MLD (Figure 1b) reflects their

¹Auxiliary materials are available in the HTML. doi:10.1029/2011GL048498.

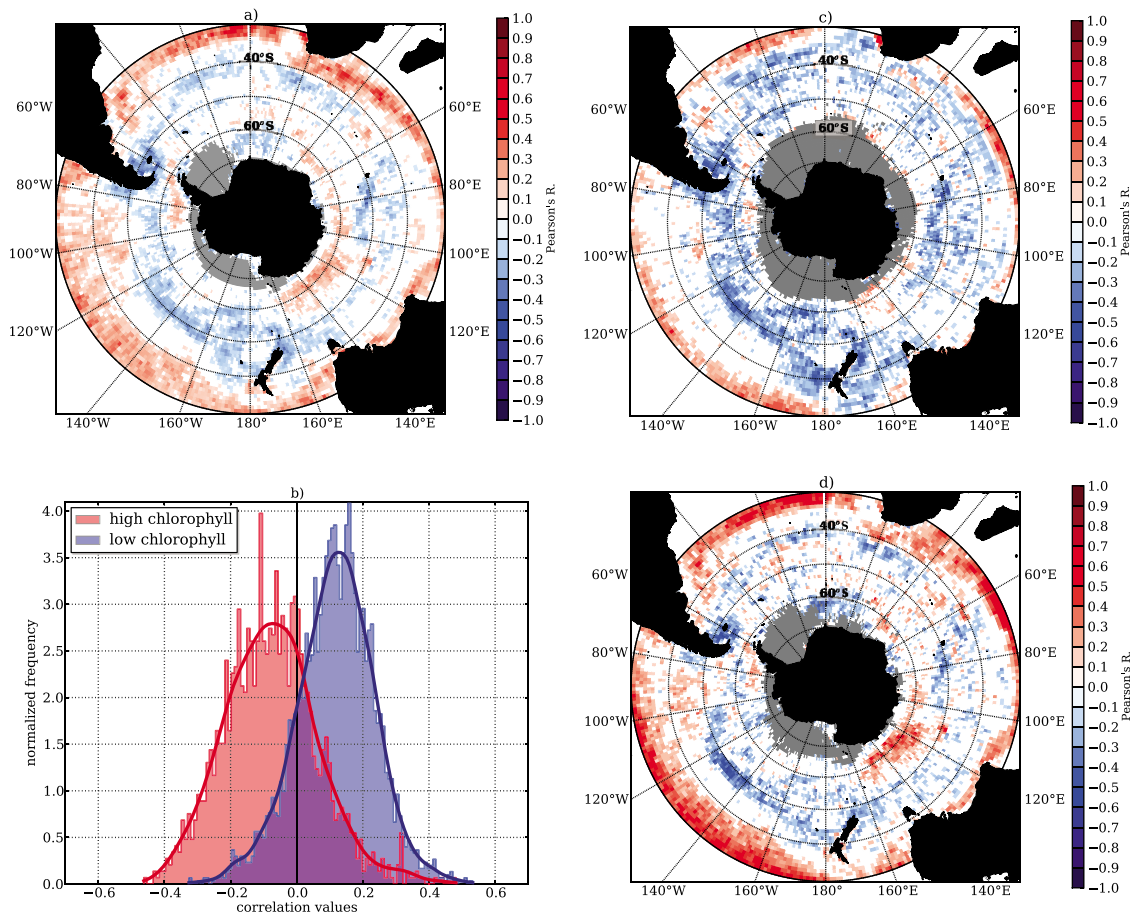


Figure 2. (a) Correlation coefficients between sub-seasonal anomalies of Chl-a and MLD during summer (October–March), regions where the correlation is found insignificant at the 90 percent confidence level (p -value > 0.1) are set to zero and appear in white, gray areas indicate more than $3/4$ of the values missing. (b) Normalized empirical distribution of the correlation coefficients between Chl-a and MLD for low ($\leq 0.15 \text{ mg}\cdot\text{m}^{-3}$) and high ($\geq 0.5 \text{ mg}\cdot\text{m}^{-3}$) Chl-a concentration regions, solid red and blue lines are a Kernel Density Estimates. Only regions experiencing a summer (October to March) peak in Chl-a concentrations (i.e., South of the Subtropical Convergence) have been included in the calculation. (c) Same as Figure 2a but for the “onset” phase (12 weeks before the peak Chl-a). (d) Same as Figure 2a but for the “decay” phase (12 weeks after the peak Chl-a).

relative phasing over the year. High and spatially coherent positive correlations North of $\sim 40^\circ\text{S}$ indicate a Chl-a maximum synchronous with deepest ML (and vice-versa), thereby delineating the subtropical, winter maxima, macro-nutrient limited regime. Generally negative correlations south of $\sim 40^\circ\text{S}$ indicate that the Chl-a maximum is synchronous with shallow MLDs, when light limitation is relieved. Note however that some areas, especially at high latitudes, present positive correlations. In contrast with the subtropical regime however, in these regions Chl-a concentrations consistently increase as the ML shoals. These positive correlations arise as a consequence of an early peak in Chl-a occurring before the minimum MLD and the absence of observations during winter (when MLD is deeper, see Figure S3 in the auxiliary material).

3.2. How Do Chl-a Concentrations Respond to Variability in MLD at Sub-seasonal Time-Scales?

[11] High positive correlations with MLD on sub-seasonal time-scales, similar to those observed on seasonal time-scales, are evident in the subtropical region, north of $\sim 40^\circ\text{S}$

(Figure 2a). Despite an austral winter peak in production, summer transient increases in Chl-a do occur and are related to a deepening of the ML (and vice-versa). This is consistent with a nutrient limited subtropical zone (north of the subtropical front, but south of 30°S) where ML deepening promotes macro-nutrient input that stimulates phytoplankton growth on both seasonal and sub-seasonal time-scales (Figures 1b and 2a).

[12] South of $\sim 40^\circ\text{S}$ (i.e., south of the STF), in the sub-Antarctic Zone and Antarctic Polar regions, the picture is more complex. The correlations with MLD are generally negative, indicating that transient episodes of increased Chl-a concentration in summer are related to a shoaling of the ML (and vice-versa) and suggest sub-optimal light conditions. This is particularly the case in the Weddell Sea (west of 20°E), downstream of the Kerguelen Islands and over the Kerguelen plateau, and in the Pacific Ocean between 50°S and 60°S . However, large areas show correlations that are insignificant (p -value > 0.1), which suggests little sensitivity of Chl-a to sub-seasonal variability in the MLD, non-linear

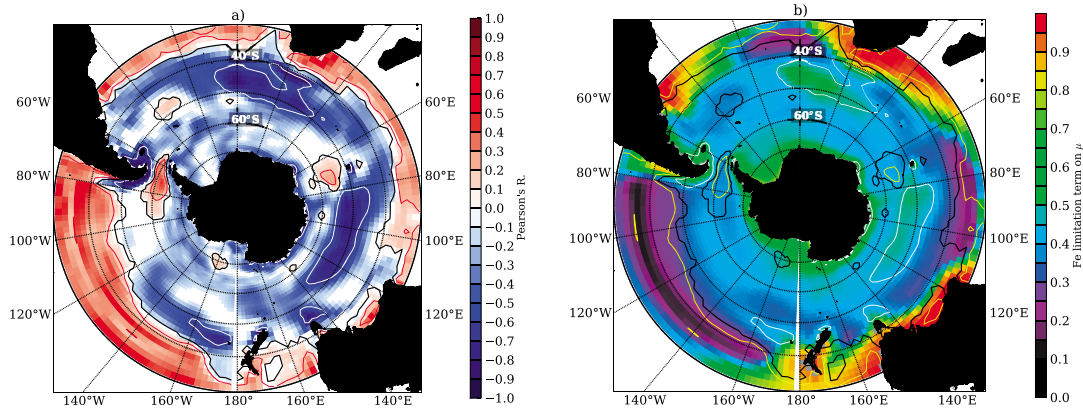


Figure 3. (a) Correlation coefficients between sub-seasonal variability (as defined as anomalies with respect to time-series convolved with a Gaussian kernel of sigma 5) of modelled Chl-a and MLD, correlations respectively greater than 0.2, equals to zero and less than -0.6 are reported and contoured in solid red, solid black and solid white. (b) Fe limitation on phytoplankton growth, calculated as the proportion of maximum growth permitted by Fe and accounts for variability in the half saturation constant between and within the two phytoplankton groups [see *Aumont and Bopp*, 2006]: a low number implies a large degree of Fe limitation. Correlations (see Figure 3a) respectively greater than 0.2, equals to zero and less than -0.6 are reported and contoured in solid yellow, solid black and solid white.

relationships (perhaps illustrating instances of top-down controls or changes to the nature of the relationship during summer) or variability occurring at time-scales shorter than 8 days. Moreover, several regions also present significant positive correlations with ML indicating that transient increases in Chl-a concentrations are related to episodes of ML deepening (and vice-versa) that indicate nutrient limitation. The large degree of spatial heterogeneity in the relationship between the sub-seasonal variability of MLD and Chl-a (negative, positive and not significant) is mirrored when the analysis is repeated using Sea-Surface-Temperature satellite estimates (Figure S4 in the auxiliary material) and raises questions about the role of MLD variability in mediating bottom-up controls on primary production at sub-seasonal time-scales.

3.3. What Dictates the Response of Chl-a to MLD Variability?

[13] The sign of the sub-seasonal correlation between MLD and Chl-a (Figure 2a) may depend on the degree of Fe limitation. If we define “low biomass” and “high biomass” regions as those exhibiting a summer average Chl-a concentrations $\leq 0.15 \text{ mg m}^{-3}$ and $\geq 0.5 \text{ mg m}^{-3}$, respectively (regions outlined in Figure 1a), we find that regions of low biomass are disproportionately positively correlated to MLD, with the opposite true for high biomass regions (Figure 2b). We propose that regions of low biomass correspond to highly Fe limited regions, where episodes of ML deepening in the summer enhance the vertical supply of Fe to the euphotic zone, triggering transient phytoplankton blooms that result in positive correlations on sub-seasonal timescales. On the other hand, regions of high biomass (see, e.g., case for downstream of Kerguelen [$\sim 48^\circ\text{S}$, 68°W] or over the South American shelf) are likely to correspond to Fe-replete environments and would tend to respond favourably to the improvement of the light conditions associated with MLD shoaling.

[14] This variable role for Fe and light in different regions of the SO is further supported when the phytoplankton growing season is divided on either side of the date of the seasonal biomass maximum (Figures 2c and 2d): low biomass regions in particular see their positive correlation increasing from the “onset” to the “decay” phase, which suggests, as expected, an increase in Fe limitation as summer progresses, while regions of negative correlations decrease, indicating a less prominent control by light.

[15] The observed variability in sub-seasonal correlations between MLD and Chl-a and its attribution is supported when examined with a complex biogeochemical model (Figure 3), which allows for an explicit calculation of the limitation on phytoplankton specific growth rates by Fe. Firstly, it is encouraging that a high degree of spatial variability in the correlation between MLD and Chl-a on sub-seasonal time-scales (positive, negative and non-significant) is also present in the model (Figure 3a). Secondly, comparing this map to the modelled Fe limitation term (Figure 3b) shows that areas of positive correlations are generally strongly Fe limited and vice versa. Only in regions where Fe permits more than half of maximum growth (i.e., not strongly Fe limited) do we see negative correlations between Chl-a and MLD. Both observations/reanalyses and model outputs thus concur and suggest that it is the balance between the mixed layer dynamics-controlled degree of light and Fe limitation that governs how the phytoplankton community responds to a transient MLD event.

3.4. Linking the Response of Phytoplankton to Variability in Bottom-up Forcing

[16] In a conceptual model valid for regions south of the STF (Figure 4), we show a water column characterised by a number of possible idealised mean seasonal MLD. The winter MLD (Z_W) reflects the deepest mixed layer resulting from winter cooling and mixing. As Z_W is deeper than the oceanic

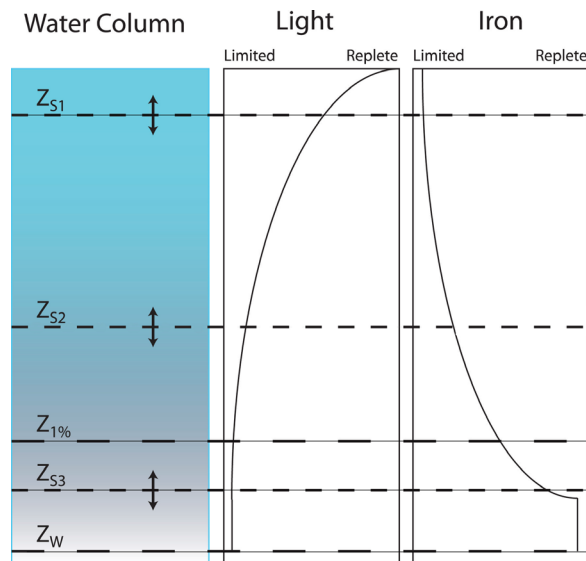


Figure 4. Conceptual model illustrating the sensitivity of phytoplankton production to sub-seasonal dynamics of the MLD in the Southern Ocean (see text for explanation). $Z_{1\%}$ = 1% light level. Z_W = winter MLD. $Z_{S1,2,3}$: possible mean seasonal MLD in relation to light and iron concentrations profiles.

ferricline (thus $> \sim 250$ m [Boyd and Ellwood, 2010]) and below the 1% light level it therefore replenishes Fe stocks in the winter ML. Although net growth rates could be positive [Behrenfeld, 2010], the low light level prevents any net phytoplankton growth. To help understand the variable response of the phytoplankton to transient events in the summer period (Oct.–Mar.), we define three scenarios (Z_{S1} – Z_{S3}), which reflect different mean seasonal depth adjustments of the summer ML to the balance between buoyancy and momentum fluxes. In areas where this balance is positive (high buoyancy forcing) the mean seasonal ML will be shallow (Z_{S1} : e.g., $< \sim 25$ m), therefore trapping a relatively small reservoir of Fe, which is rapidly exhausted under near saturating light conditions during biomass accumulation. Biomass decays via settling or grazing and the re-supply of Fe from a ML deepening, followed by rapid shoaling of the ML driven by high seasonal buoyancy fluxes, initiates the next transient bloom event. This mechanism could be at play in regions showing positive correlations between MLD and Chl-a, where light is replete and Fe stocks are low, i.e., the low biomass (Fe limited) regions of the SO. In sharp contrast, in the third mixed layer scenario (Z_{S3}), the balance between seasonal buoyancy and mixing again results in a MLD close to or deeper than the euphotic depth (i.e., deeper than Z_{S2} , but shallower than Z_W). This provides the mixed layer with a relatively large reservoir of Fe but sub-optimal light conditions. Accordingly, in this scenario the ML needs to shallow during quiescent wind periods to relieve light limitation and enhance biomass, corresponding to areas of negative correlation between MLD and Chl-a. The regions characterised by weak correlations are those where the mean summer buoyancy – mixing balance (Z_{S2}) is deeper than Z_{S1} but shallower than the depth of the 1% light level (a proxy for the depth of the ‘euphotic zone’). Here, the summer reservoir of Fe is larger than at Z_{S1} and light remains largely non-limiting,

which means that the system does not respond to changes in bottom up forcing as mediated by MLD variability.

[17] We note that Z_{S1} – Z_{S3} are conceptual and that their precise depth will depend as much on the mean seasonal balance between buoyancy and momentum on the one hand and on the local Fe profile and light conditions on the other hand. It is expected to be variable in space and time. Moreover, our model rests on the assumption of dominant vertical Fe supply and bottom-up controls. The response may be more complex in regions where surface fluxes of Fe from dust deposition are significant or conditions where control by grazing is prominent. That said, it does provide a mechanistic explanation for a wide spread of results that we find (positive, negative, not significant, Figure 2a) regarding the correlations between Chl-a and MLD on sub-seasonal timescales.

4. Conclusions

[18] In conclusion, we find a large spatial (as well as seasonal) variability in the nature of the response of Chl-a concentrations to transient MLD variability in the Southern Ocean, both in the observations / ocean reanalyses and in a complex biogeochemical model. Our results suggest that the strength of iron limitation, relative to light, seems to be instrumental in dictating these patterns. In a conceptual model we propose that it is the depth of the seasonal ML, relative to the balance between light and Fe vertical profiles, that governs how the phytoplankton responds to transient events. We highlight that the various (and sometimes opposite) relationships between ML and phytoplankton biomass variability depending on the time-scale considered (seasonal versus sub-seasonal) have important implications regarding the response of primary production to the predicted, and already observed, trends in the SO buoyancy forcing and stratification in response to climate change [see Gille, 2002; Boyce *et al.*, 2010]. From a modelling perspective it is encouraging to note that NEMO-PISCES (an IPCC class model) does indeed share property – property relationships similar to observations, thus allowing us to investigate these issues further. This will require a consideration of the strength of stratification (which will impact vertical supply of Fe), the regional characteristics of the Fe cycle (particularly external sources), inclusion of the variability in Silica limitation (especially north of the Polar Front), as well as the role played by grazing modulation in response to MLD variability (i.e., ‘top down’ controls).

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