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## **Delineating environmental control of phytoplankton biomass and phenology in the Southern Ocean**

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3 **Delineating environmental control of phytoplankton biomass and**  
4 **phenology in the Southern Ocean**  
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26 **Main point #1:** Phytoplankton phenology and biomass are mostly organized in the  
27 Southern Ocean at a large latitudinal scale and a regional scale.  
28

29 **Main point #2:** The timing of bloom occurrence appears tightly linked to the seasonal  
30 cycle in irradiance, with some exceptions in specific light-limited regimes.  
31

32 **Main point #3:** Zonal asymmetries in regional-scale phytoplankton biomass are mainly  
33 driven by local advective and iron supply processes.  
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36 **Running head (40 characters max):** Phytoplankton dynamics in the SO  
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44

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46 **Abstract**

47 The Southern Ocean (SO), an area highly sensitive to climate change, is currently experiencing  
48 rapid warming and freshening. Such drastic physical changes might significantly alter the SO's  
49 biological pump. For more accurate predictions of the possible evolution of this pump, a better  
50 understanding of the environmental factors controlling SO phytoplankton dynamics is needed.  
51 Here we present a satellite-based study deciphering the complex environmental control of  
52 phytoplankton biomass (PB) and phenology (PH; timing and magnitude of phytoplankton  
53 blooms) in the SO. We reveal that PH and PB are mostly organized in SO at two scales: a large  
54 latitudinal scale, and a regional scale. Latitudinally, a clear gradient in the timing of bloom  
55 occurrence appears tightly linked to the seasonal cycle in irradiance, with some exceptions in  
56 specific light-limited regimes (i.e. well-mixed areas). Superimposed on this latitudinal scale,  
57 zonal asymmetries, up to three orders of magnitude, in regional-scale PB are mainly driven by  
58 local advective and iron supply processes. These findings provide a global understanding of PB  
59 and PH in SO, which is of fundamental interest for identifying and explaining ongoing changes  
60 as well as predicting future changes in the SO biological pump.

61

62 **1. Introduction**

63 The Southern Ocean (SO) plays a key role in the global carbon cycle, absorbing 40% of the  
64 total oceanic inventory of anthropogenic CO<sub>2</sub> [*Khaliwala et al.*, 2009]. However, current and  
65 predicted changes in ocean circulation and hydrology associated with climate variability might  
66 impact the efficiency of the SO carbon sink, although the extent of such changes and their  
67 specific impact on the biological pump are still vigorously debated [*Landschützer et al.*, 2015; *Le*  
68 *Quéré et al.*, 2010; *Munro et al.*, 2015]. Such debate cannot advance without a better

69 understanding of the factors that shape the complex biogeography of the SO, and what controls  
70 their time-scale of variability (i.e. daily, seasonal to decadal).

71 Delimiting marine bio-regions has proven highly valuable for disentangling multiple  
72 limiting growth factors affecting the efficiency of the biological pump [Longhurst, 2007]  
73 mediated by both PB and PH, and for ultimately underlining effects of climate change such as  
74 areal changes in trophic regime [Polovina *et al.*, 2008] or in fisheries stock and species  
75 [Fossheim *et al.*, 2015]. Changes in PB profoundly alter the efficiency of the biological pump,  
76 thereby modulating energy transfer to upper trophic levels and carbon export to deep water  
77 [Legendre and Rassoulzadegan, 1995]. Changes in PH may also have important consequences  
78 for the marine food web, due to potential mismatch between primary and secondary producers  
79 and apex predators [Ardyna *et al.*, 2014; Edwards and Richardson, 2004], and for the carbon  
80 cycle through export of unexploited carbon aggregates to the deep ocean [Dall'Olmo *et al.*,  
81 2016].

82 The efficiency of the SO's biological pump is strongly associated with phytoplankton  
83 biomass (PB) and its phenology (PH), which themselves are mediated by nutrient availability  
84 (e.g. mainly iron, and/or possibly nitrate and silicic acid), light, temperature and mortality factors  
85 [Behrenfeld and Boss, 2014; Boyd, 2002]. These factors are essentially controlled by vertical  
86 mixing, advection, seasonal fluctuations in solar irradiance, and the extent and typology of sea-  
87 ice cover. As a result, a variety of patterns of net primary production (NPP) are found in the SO  
88 [Arrigo *et al.*, 2008], with their own associated phytoplankton species succession, stock, and  
89 distribution [Quéguiner, 2013]. Delineating the interplay of environmental forcing on PB and PH  
90 remains challenging and requires novel approaches, which are available through satellite-derived  
91 observations. Using these integrative and multidisciplinary approaches (i.e. satellite-derived

92 ocean color and altimetry, Argo floats, lagrangian modeling and biogeographic-derived  
93 analysis), we provide here a global understanding of the phytoplankton biomass and phenology  
94 in a potentially changing SO.

## 95 **2. Material and methods**

### 96 2.1 Satellite-derived, climatological and modeling products

97 Satellite-derived Level-3 data sets of chlorophyll-a concentration ( $\text{chl } a$ ;  $\text{mg m}^{-3}$ ) and  
98 photosynthetically available radiation (PAR;  $\text{E m}^{-2} \text{d}^{-1}$ ) were obtained from the European Space  
99 Agency's GlobColour project (<http://www.globcolour.info>). Eight-day composite  $\text{chl } a$   
100 concentrations using standard Case 1 water algorithms were used (i.e. OC4v5 for SeaWiFS,  
101 OC4Me for MERIS and OC3v5 for MODIS/VIIRS sensors; see *O'Reilly et al.* [2000] and  
102 *Maritorena et al.* [2010] for details). The climatological annual net primary production (NPP)  
103 was derived from the adapted-SO NPP model of *Arrigo et al.* [2008]. A detailed description of  
104 the NPP model can be found in the supporting information [*Dobson and Smith*, 1988; *Gregg and*  
105 *Carder*, 1990; *Markus*, 1999]. The climatologies of mixed layer depth and bathymetry were  
106 extracted respectively from *Pellichero et al.* [2016] and the GEBCO, version 2014 (General  
107 Bathymetric Chart of the Oceans; <http://www.gebco.net>). The climatology of the length of the  
108 sea-ice cover was derived from the Special Sensor Microwave Imager (SSM/I; 1998–2002) and  
109 the Advanced Microwave Scanning Radiometer - Earth Observing System (AMSR-E; 2002–  
110 2014) sensors, and made available by National Snow and Ice Data Center (NSIDC;  
111 <https://nsidc.org>). The locations of the major fronts (i.e. the Subantarctic Front SAF, the  
112 Antarctic Polar Front APF, the Southern Antarctic Circumpolar Current (ACC) Front SACCF  
113 and the Southern Boundary of the ACC SBdy, following *Swart et al.* [2010]) were determined  
114 based on the Maps of Absolute Dynamic Topography (MADT) product from CLS/AVISO. The

115 Lagrangian model of horizontal dispersion of iron fluxes used also altimeter products produced  
116 by CLS/AVISO, with support from the CNES (Centre National d'Etudes Spatiales;  
117 <http://www.aviso.altimetry.fr/duacs/>).

## 118 2.2. Clustering K-means method

119 The bio-regions were defined here using a cluster K-means analysis (see the SI for more  
120 details), previously applied successfully in the Mediterranean Sea [*D'Ortenzio and Ribera*  
121 *d'Alcalà, 2009; Mayot et al., 2016*], in the North Atlantic [*Lacour et al., 2015*] and at the global  
122 scale [*D'Ortenzio et al., 2012*]. The analysis was performed on climatological and normalized  
123 annual chl *a* cycle, in order to statistically organize the GLOBcolour time series (1998–2014)  
124 and to create clusters representing regions of similarity (i.e. annual chl *a* cycles). To maintain  
125 consistency in the seasonal data availability throughout the study area, the period study covers  
126 the period from September to March (as referred here to “annual”). This technique regroups  
127 pixels with seasonal cycles shapes - i.e. similar phenologies. A single characteristic seasonal  
128 cycle, that is statistically representative of the group as a whole, is then determined by  
129 calculating the center (average cycle) within each group or cluster. Each group representative of  
130 a characteristic seasonal cycle constitutes a phenological characteristic regime. A more detailed  
131 discussion of the cluster K-means analysis can be found in the supporting information [*Devred et*  
132 *al., 2007; Hartigan and Wong, 1979; IOCCG, 2009; Lund and Li, 2009; Milligan and Cooper,*  
133 1985]

134 A one-way analysis of variance by ranks (Kruskal–Wallis H test; *Zar [2010]*) was  
135 performed to test whether eco-regions differed in their biological characteristics (i.e. annual  
136 mean chlorophyll *a* concentration, seasonality and timing of bloom). A significant result of the  
137 Kruskal–Wallis H test implies that at least one eco-region differs from all others.

## 138 2.3 Lagrangian modeling of horizontal iron fluxes

139 In order to estimate iron delivery due to horizontal stirring, we use an advection scheme  
140 based on altimetry, extending to the Southern Ocean a Lagrangian model used for predicting the  
141 development of the Kerguelen phytoplanktonic plume [*d'Ovidio et al.*, 2015]. The model has  
142 been extensively calibrated and validated in the Crozet and Kerguelen regions by integrating  
143 satellite data (altimetry and ocean color), lithogenic isotopes, iron measurements, and drifters  
144 [*d'Ovidio et al.*, 2015; *Sanial et al.*, 2014; *Sanial et al.*, 2015]. The main characteristics of the  
145 model were resumed here and we refer to *d'Ovidio et al.* [2015] for the full description of the  
146 model. The model seeds each open ocean location with a particle and finds the particle's most  
147 recent contact with a shallow bathymetry by a back-trajectory issued from altimetry data. It  
148 provides the time and the position at which the contact took place. An exponential scavenging  
149 relation (with a time constant based on in situ iron data from the KEOPS2 cruise) is used to  
150 estimate the decreasing of bio-available iron along the trajectory from the time of the contact  
151 with the potential iron source to the current position. Here, the model was applied to the entire  
152 Southern Ocean using a grid of  $0.25^\circ$ , a time window of 2004-2015 (one map every 4 days),  
153 potential sources of iron in the bathymetric band shallower than 500m, and a diffusion term of  
154  $40 \text{ m}^2 \text{ s}^{-1}$ .

155

## 156 **3. Results and discussion**

157 Based on satellite-derived observations, a large range of both annual mean chlorophyll *a*  
158 (chl *a*) concentration and net primary production (NPP) ( $>0.1 \text{ mg chl } a \text{ m}^{-3}/20 \text{ g C m}^{-2} \text{ y}^{-1}$  to  
159 more than  $2 \text{ mg chl } a \text{ m}^{-3}/400 \text{ g C m}^{-2} \text{ y}^{-1}$ , respectively) were observed across the SO. It occurs  
160 at a variety of scales, including the latitudinal and the regional (i.e. Indian, Pacific and Atlantic;

161 Fig. 1a) scales in the SO. The annual mean chl *a* concentration is associated with the amplitude  
162 of its seasonal cycle (Fig. 1a&c). In contrast, the timing of blooms (i.e. the maximum of the  
163 annual chlorophyll cycles, Fig. 1d) appears entirely decoupled from both large-scale patterns in  
164 annual chl *a* concentration and its seasonality (Fig. 1c), hence revealing a complex organization  
165 of phenological patterns of the chl *a* annual cycle.

166 Here, we disentangle the spatial complexity of chl *a* seasonal cycle using a K-mean  
167 clustering method [D'Ortenzio *et al.*, 2012] with the goal of defining distinct bio-regions with  
168 similar large-scale patterns in PH (Fig. 2). In brief, this technique statistically gathers regions  
169 that exhibit similarly shaped seasonal chl *a* cycles (see the section 2.2 for more details). The  
170 seven distinct bio-regions so identified are distributed along a latitudinal gradient (Fig. 3a). At  
171 temperate latitudes, two bio-regions (i.e. 1 and 2) exhibit an early bloom in October. Moving  
172 south to 45-63°S, two other bio-regions (i.e. 4 and 5) display an annual chl *a* cycle with a  
173 delayed bloom in November/December. Finally, near the Antarctic continental shelf (< 63°S),  
174 the dominant bio-regions 6 & 7 were characterized by a late bloom in January/February.  
175 Interestingly, one bio-region (i.e. 3) differs drastically from the general phenological trend of a  
176 delayed bloom moving from subtropical to polar latitudes, having a late bloom at a moderate  
177 latitude ( $\approx 43^\circ\text{S}$ , Fig. 2 & 3d). Furthermore, the co-existence of bio-regions at a same latitude  
178 indicates variations in the seasonality of the annual chl *a* cycle (e.g., 1 & 2, 4 & 5 and 6 & 7)  
179 which are related to distinct levels of PB (Figs 3b-c).

180 From temperate to high latitudes, the latitudinal gradient in bloom timing clearly follows  
181 changes in light regime (expressed as the annual mean photosynthetically available radiation in  
182 the double boxplot; Fig. 4a). The unique bio-region (i.e., 3), characterized by a paradoxically late  
183 bloom with respect to the timing of light availability, is mainly located in the vicinity of the

184 Antarctic Circumpolar Current. Interestingly, this region corresponds to the highest Southern  
185 Ocean wind stress and depth of the mixed layer (see SI, Fig. S1). Deep mixed-layers likely  
186 impose severe light limitation to phytoplankton growth in spring, hence delaying the bloom later  
187 in season. Close to the Antarctic shelf, as shown locally in the western Antarctic Peninsula  
188 [Venables *et al.*, 2013], the timing of the bloom (Fig. 2) was not related to winter sea-ice extent  
189 but more to the seasonal cycle of irradiance.

190 To address the potential causes of regional-scale variability in PB (Fig. 1a), we hypothesize  
191 that iron availability represents its first order driver [Hutchins and Boyd, 2016]. Using integrative  
192 and multidisciplinary approaches, we disentangle the impact of four important iron supply  
193 mechanisms on PB. These surface-layer iron-sources are shallow plateaus (<500 m) which both  
194 (i) locally recharge the surface-layer in iron [Arrigo *et al.*, 2015; Graham *et al.*, 2015] and (ii)  
195 remotely recharge the surface layer by lateral advection of non-consumed iron [d'Ovidio *et al.*,  
196 2015; Graham *et al.*, 2015]; (iii) sea-ice, which recharges the surface as ice melts [Arrigo *et al.*,  
197 2015; Lannuzel *et al.*, 2016]; and (iv) vertical mixing through deep convection, which can  
198 entrain iron from deep water [Tagliabue *et al.*, 2014b]. Below, the potential impact of these four  
199 likely iron-sources on the intensity of PB is investigated. Note that the Aeolian iron deposition  
200 was not considered here as a major iron supply mechanism due to its intermittency and its  
201 unclear role in regulating PB [Boyd *et al.*, 2012; Cassar *et al.*, 2007; Tagliabue *et al.*, 2009;  
202 Tagliabue *et al.*, 2017].

203 Clearly, the highest PB ( $> 1.2 \text{ mg m}^{-3}$ ) are detected in shallow areas (< 500 m), on  
204 continental and island shelves where iron fluxes are expected to be significant [Boyd *et al.*, 2012;  
205 Tagliabue *et al.*, 2014a]. Furthermore, we use a Lagrangian model based on altimetry in order to  
206 track which water parcels have been recently in contact with a shallow area – and when – to

207 assess the probable locations of some of the iron plumes downstream of these iron sources and to  
208 estimate their loss of bio-available iron during advection by scavenging [*d'Ovidio et al.*, 2015].  
209 We find a well-defined decline in PB (from 0.8 to 0.3 mg m<sup>-3</sup>) with distance and time from the  
210 most recent contact of the water parcel with a shallow area (Fig. 4b): the further away a water-  
211 parcel is from the initial shallow area iron source, or the longer after a water-parcel has been  
212 iron-enriched in shallow areas, the weaker is the PB signal. We note however that seamounts and  
213 submerged plateaus do not enhance local or downstream PB, as already observed north of  
214 Kerguelen plateau [*Graham et al.*, 2015] (Figs. 1a&4c), suggesting that not all shallow areas are  
215 active and/or bioavailable iron sources. Close to the Antarctic shelf and coastal polynyas, the  
216 potential role of the seasonal melting of sea-ice [*Arrigo et al.*, 2015; *Lannuzel et al.*, 2016] as  
217 iron source is revealed with enhanced PB ( $\approx 0.4$  mg m<sup>-3</sup>).

218 Moving away from potential iron delivery from shallow areas (either locally or  
219 downstream) and from sea-ice, we investigated the possible role of mixed-layer depth on  
220 regulating PB. If deepening of the mixed layer in winter can recharge the surface layer in  
221 nutrients (iron, but also nitrate and silicic acid in the temperate regimes) by deep convection, it  
222 can also limit PB by reducing light availability for phytoplankton growth during the growing  
223 season. Indeed, region of deep winter mixing in the Southern Ocean are mostly located directly  
224 north of the ACC, where strong winds and isopycnal tilts, are associated with an season-wide  
225 weak stratification, leading to deep winter mixed layer but also to relatively deep, compared to  
226 their surrounding, spring and summer mixed-layers.

227 Our findings clearly translate this complex interplay between availability of nutrient and  
228 light related to the winter mixed-layer depth. An increase in PB is observed with the deepening  
229 of the winter mixed-layer until a maximum winter depth of about 150 m. When the winter mixed

230 layer becomes deeper, a decrease in PB is observed, likely resulting from a stronger light  
231 limitation of phytoplankton growth during the growth season (Sep-Mar; on average, winter  
232 mixed layer deeper than 150 m are associated to Sep-Mar mixed layer deeper than 110 m or so;  
233 Fig 4b). We thus depict here a tipping winter MLD at ~ 150m, which likely represents a shift  
234 between an iron-limited to a light-limited environment. Such threshold in the MLD is certainly  
235 dependent on the local structure of the iron profile [Tagliabue *et al.*, 2014b]. Despite the HNLC  
236 (High Nutrient Low Chlorophyll) nature of the Southern Ocean, an intermediate mixing mode  
237 (i.e., with a winter MLD maximum from 120 to 200 meters) appears to enhance PB by supplying  
238 an optimal combination of both light and nutrient requirements for phytoplankton growth. This  
239 apparently modest effect of optimal mixing on PB may nevertheless have major implications due  
240 to the large areal extension of those zones relying on the vertical mixing to support  
241 phytoplankton iron requirements (Fig. 4c).

242 Deciphering the complexity of the SO's phytoplankton phenology and biomass is  
243 particularly critical to assess how climate variability and change might regionally impact the  
244 biological pump. Our results reveal two main scales of organization for both PB and PH, i.e. a  
245 large latitudinal and a regional scale. Alterations of stratification that are expected with global  
246 warming may modify light-mixing regimes, and thus potentially modulate the bloom timing.  
247 However, since the phenology appears here to be strongly linked to the circumpolar seasonal  
248 cycle in irradiance, we suppose that only drastic changes in stratification could significantly alter  
249 bloom timing, and therefore the impact on the biological pump might be expected to be relatively  
250 minor.

251 Concerning the fate of phytoplankton biomass in the changing SO, no particular changes at  
252 local scale are expected in shallow bathymetry (i.e. where iron recharge from shallow plateaus

253 (<500 m) are not prone to be affected). Potential changes also likely to remain minor in  
254 downstream transport from ACC, depending on whether the ACC has shifted locally in some  
255 regions over the past decades according to climate model [*Kim and Orsi, 2014; Sallée et al.,*  
256 2008] but not others [*Gille, 2014; Shao et al., 2015*]. Even if ACC changes remain unclear under  
257 next century climate change scenarios [*Meijers et al., 2012*], past studies indicate that if there is a  
258 change, the expected position change should be small compared to the size of the bathymetry  
259 structure it interacts with to give rise to ocean surface iron plumes.

260 The main uncertainties regarding the fate of PB thus remains linked to the role of the  
261 mixed-layer depth and the sea-ice, which have a more direct response to climate variability and  
262 change. Climate modes have direct regional impact on both sea-ice and mixed-layer depth  
263 [*Sallée et al., 2010; Simpkins et al., 2012*]. In response to SAM and ENSO, sea-ice extends in  
264 some regions and is reduced in others, which, according to our results, would have regional  
265 impact on iron delivery and PB intensity. Similarly, SAM tends to deepen mixed-layer depth  
266 regionally but shallows it in other regions. Under next century climate change, the response is  
267 more regionally consistent, with an overall shallowing of the mixed-layer associated with  
268 increased stratification (freshwater input from glacier and sea-ice, and increased heat forcing  
269 from the atmosphere), and an overall reduction of sea-ice cover.

270 However, according to our findings, a shallowing (or deepening) of the mixed-layer is not  
271 expected to translate to the same PB response everywhere (see SI, Fig. S2). Indeed, the response  
272 would be state-dependent: a shallowing of a deep mixed-layer (typically deeper than 200 m)  
273 would result in an increase in PB, while a shallowing of an already relatively shallow mixed-  
274 layer (typically less than 120 m), would reduce PB. At the SO scale, a global shallowing of the  
275 mixed-layer depth appears to have negative consequences on PB (loss of  $\approx 0.3 \% \text{ m}^{-1}$ ; see SI),

276 mainly due to the areal increase of depleted-iron regions with less efficient vertical iron recharge.  
277 Conversely, a positive response of PB (increase of  $\approx 0.15 \text{ \% m}^{-1}$ ; see SI) would be observed with  
278 a global deepening of the mixed-layer until a critical threshold (+40 m compared to the actual  
279 mixed-layer depth climatology), from which severe light limitation damps phytoplankton growth  
280 and biomass. Given the more direct response of the MLD to climate variability and change in the  
281 SO, these results highlight the crucial role of the local vertical mixing and the associated subtle  
282 balance between light/nutrient availability on regulating PB in the majority of the HNLC areas of  
283 the SO.

284

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293

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427

### Figure captions

428

429 **Figure 1: Phytoplankton biomass, net primary production and phenology in the Southern**

430 **Ocean.** Map showing the climatological (a) annual mean chlorophyll *a* concentration ( $\text{mg m}^{-3}$ ),

431 (b) annual net primary production ( $\text{g C m}^{-2} \text{d}^{-1}$ ), (c) the chlorophyll *a* seasonality ( $\text{mg m}^{-3}$ ), (d)

432 the timing of the bloom (week) maximum based on the GLOBcolour time series (1998–2014).

433 The climatological annual net primary production (b;  $\text{mg C m}^{-2} \text{d}^{-1}$ ) was derived from the

434 adapted-SO NPP model of Arrigo et al. (2008). Frontal positions calculated from MADT

435 contours are shown for the STF (white), the SAF (red), the PF (yellow) and the SACCF (black).

436

437 **Figure 2: Biogeography of the Southern Ocean.** Spatial distribution (a) of the 7 bio-regions

438 (i.e. bio-regions 1 to 7) of the Southern Ocean obtained from the k-means analysis. The

439 normalized annual chlorophyll cycles (continuous lines) of the centers of the clusters (b – h)

440 obtained from the k-means analysis are presented, as well as their respective standard deviation.

441 The absolute annual chlorophyll cycles (dashed lines) corresponding to the centers of the clusters

442 (b – h) are also indicated.

443

444 **Figure 3: Latitudinal repartition of the bio-regions and their respective biological**

445 **characteristics.** Latitudinal proportion (a) of the different bio-regions. Box plots of the bio-

446 regions (1 to 7; x axis) against (b) annual mean chlorophyll *a* concentration ( $\text{mg m}^{-3}$ ), (c) the

447 chlorophyll *a* seasonality ( $\text{mg m}^{-3}$ ), (d) the timing of the bloom maximum (month; y axis). The

448 line in the middle of each box represents the region median. The top and bottom limits of each

449 box are the 25th and 75th percentiles, respectively. The lines extending above and below each

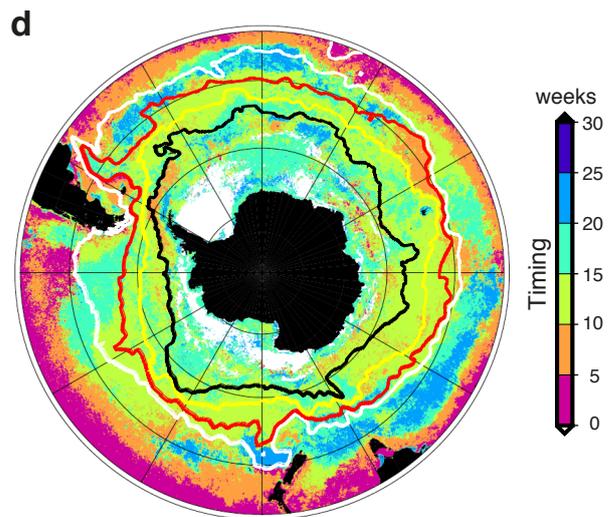
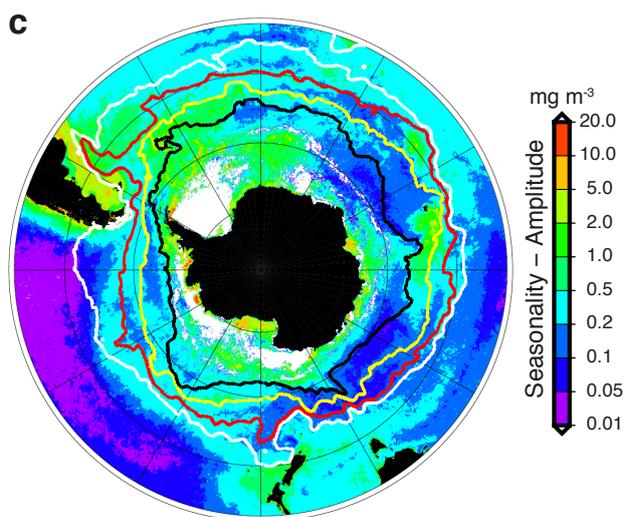
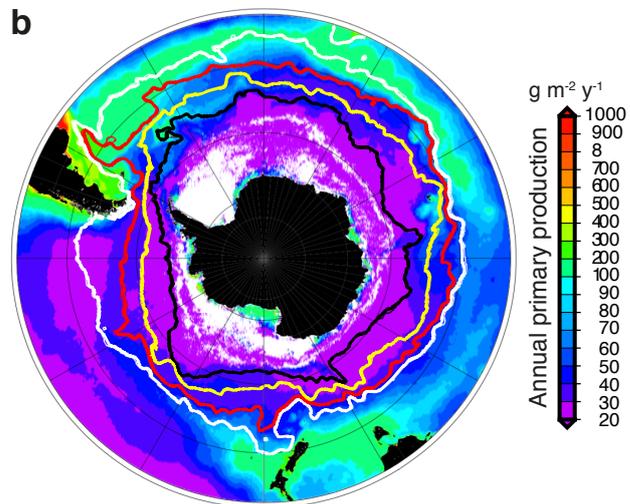
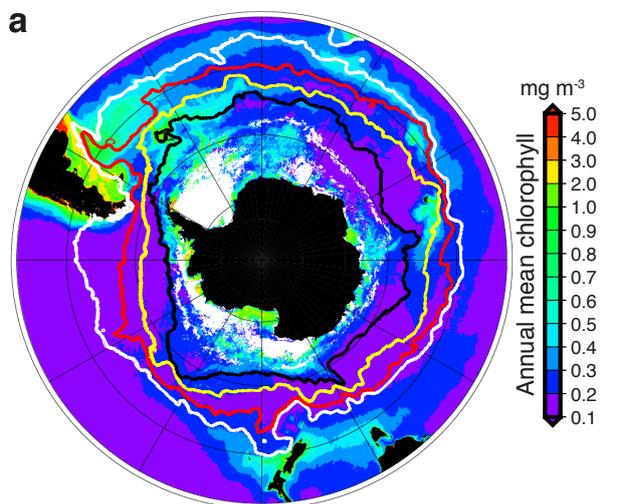
450 box, i.e., whiskers, represent the full range of non-outlier observations for each variable beyond  
451 the quartile range. The results of the Kruskal–Wallis H test are shown in figures (b) through (d),  
452 and depict regions with statistically significant differences between the climatological input  
453 variables at the 95 % level ( $p < 0.05$ ). The codes of the test significance are as follow .:  $p < 0.05$ ,  
454 \*:  $p < 0.01$ , \*\*:  $p < 0.001$  and \*\*\*:  $p < 0.0001$ .

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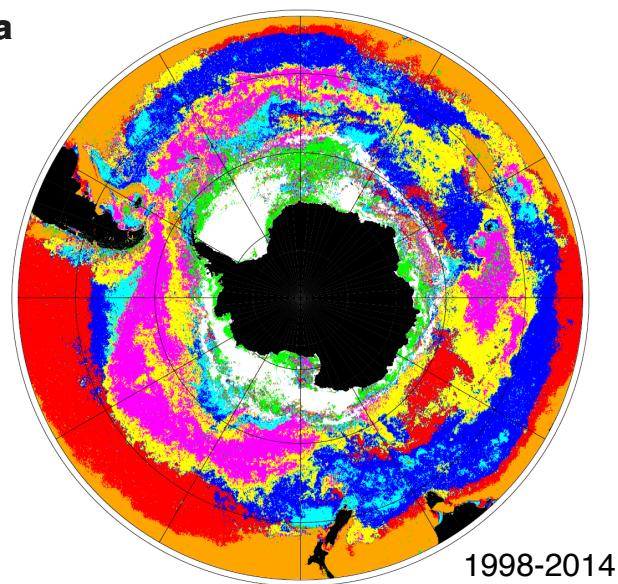
456 **Figure 4: Environmental control of phytoplankton biomass and phenology in the Southern**  
457 **Ocean.** Double boxplot (a) of the maximum bloom timing (weeks) versus the annual mean PAR  
458 ( $E\ m\ y^{-1}$ ) of the different bio-regions. The top/right and bottom/left limits of each box are the  
459 25th and 75th percentiles, respectively. The numbers in each box are located at the median of  
460 both maximum bloom timing and annual mean PAR. Barplot (b) of the mean annual  
461 chlorophyll *a* concentration according (1) the shallow areas ( $< 500\ m$ ; red), (2) areas where iron  
462 delivery downstream take place (%; percent of iron remaining in a water parcel after scavenging  
463 in respect to its initial concentration acquired in shallow areas; red to blue), (3) areas  
464 characterized by a seasonal sea-ice cover (grey) and (4) areas where variations in the annual  
465 maximum MLD are analyzed (white). See the map (c) delineating the distinct areas listed just  
466 above.

467

**Figure 1.**



**Figure 2.**

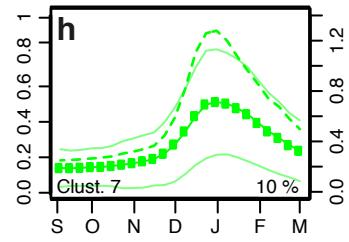
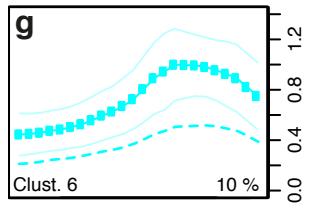
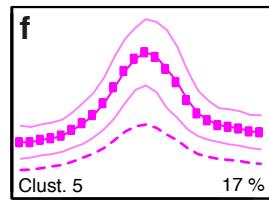
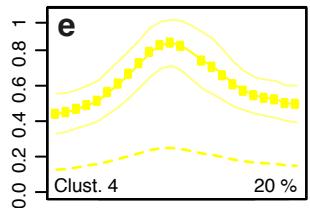
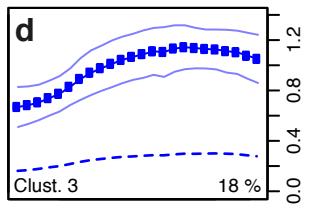
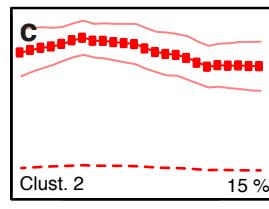
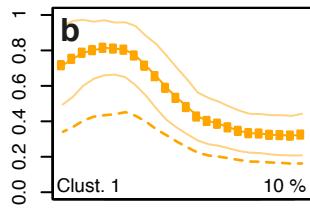
**a**

Index

Bio-region

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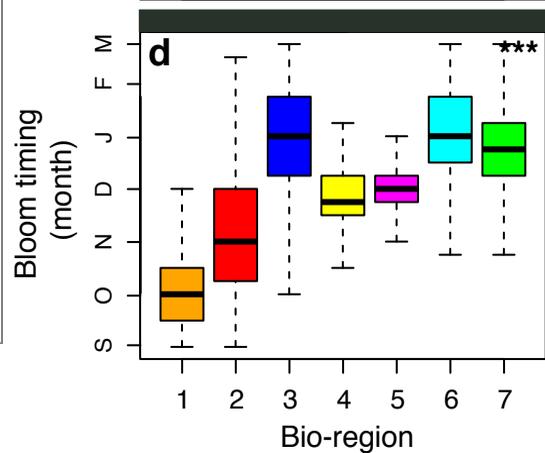
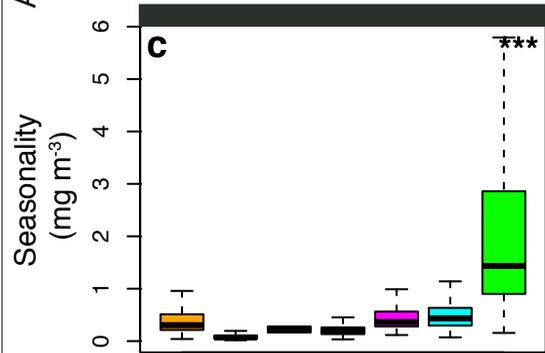
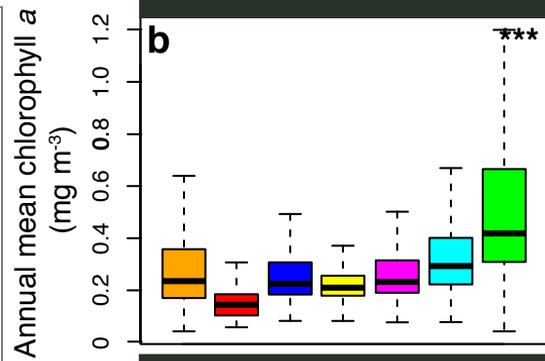
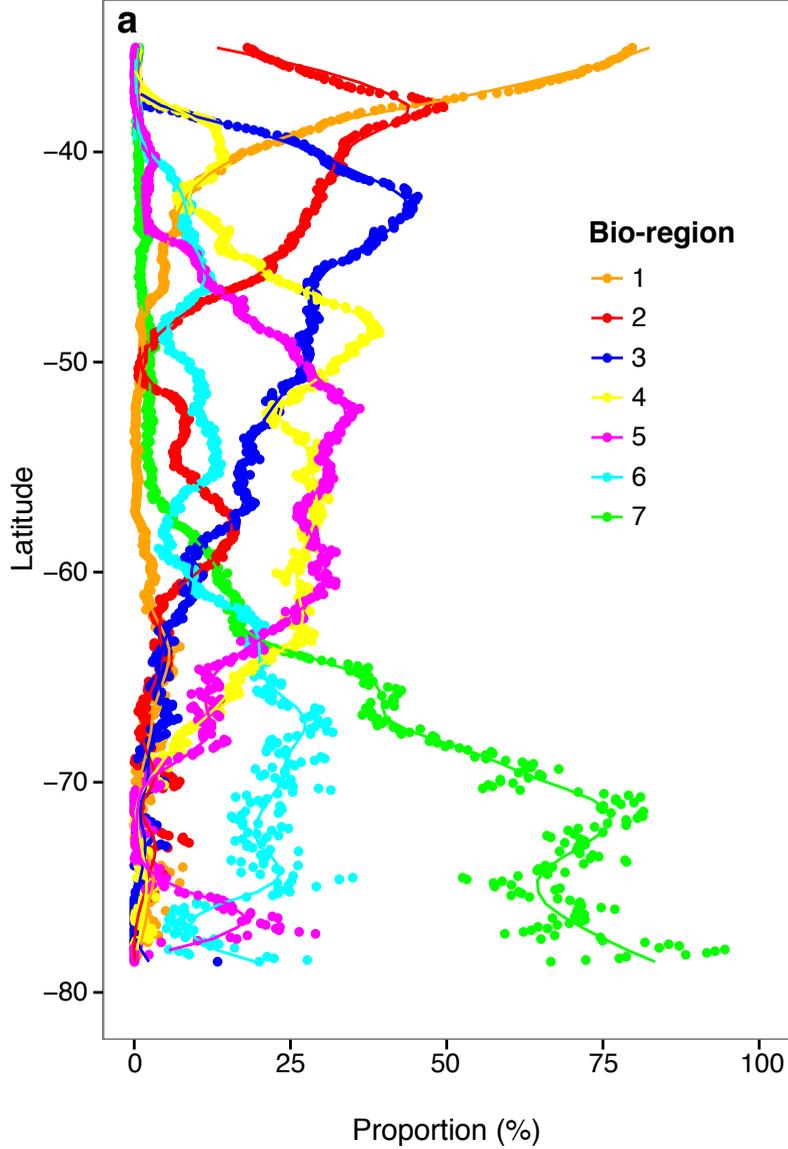
1998-2014

Normalized chlorophyll *a*Absolute chlorophyll *a* (mg m<sup>-3</sup>)

Month

S O N D J F M

**Figure 3.**



**Figure 4.**

