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1 **Non-monotonic response of primary production and export to changes in**
2 **mixed-layer depth in the Southern Ocean**

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11 **Key Points:**

- 12 • Moderate shoaling of winter mixed layer causes increase in primary production but
13 shoaling below a threshold depth can lead to a collapse.
- 14 • Reversal in this response is due to balancing effects of iron and light limitation and
15 associated with a change in community structure and export efficiency.
- 16 • Interestingly, shoaling summer mixed layer always reduces PP and export because of a
17 reduction of the productive volume.

18

19 **Abstract**

20 Ongoing and future changes in wind and temperature are predicted to alter upper ocean vertical
21 mixing across the Southern Ocean. How these changes will affect primary production (PP)
22 remains unclear as mixing influences the two controlling factors: light and iron. We used a large
23 ensemble of 1D-biogeochemical model simulations to explore the impacts of changes in mixed-
24 layer depths (MLD) on PP in the Southern Ocean. In summer, shoaling MLD always reduced
25 depth-integrated PP, despite increasing production rates. In winter, shoaling mixed-layers had a
26 two-staged impact: for moderate shoaling PP increased as light conditions improved, but more
27 pronounced shoaling decreased iron supply, which reduced PP. The fraction of PP exported
28 below 100m also presented a non-monotonic behavior. This suggests a potential future shift from
29 a situation where reduced winter mixing increases PP and export, to a situation where PP and
30 export may collapse if the ML shoals above a threshold depth.

31

32 Plain Language Summary

33 In the Southern Ocean, atmospheric warming associated to climate change is altering the depth at
34 which surface waters are stirred, the so-called *mixed-layer depth*. A change in the *mixed-layer*
35 *depth* impacts the phytoplankton cells that inhabit it by altering their two main limiting factors:
36 iron and light. However, the sign and magnitude of this impact are still not clear. In this work we
37 used mathematical simulations to explain how changes in the seasonal *mixed-layer depth* modify
38 the supply of iron and the amount of light, and how these changes impact phytoplankton activity.
39 Our results show that *mixed-layer depth* changes in summer and in winter have different impacts.
40 Reducing summer *mixed-layer depth* did not change the iron supply but it reduced the volume of
41 water where phytoplankton thrived. In winter, shallower *mixed-layer depth* altered iron and light
42 but in opposed ways. At first, phytoplankton increased its activity as more light became
43 available. However, a continued shallowing of the *mixed-layer depth* eventually reduced the iron
44 supply and the phytoplankton activity. Our study proposes a new interpretation on how ongoing
45 changes in the Southern Ocean impact phytoplankton activity and alerts of the presence of
46 threshold depths for the winter mixed-layer above which phytoplankton may struggle to survive.

47

48 **1 Introduction**

49 Southern Ocean (SO) atmospheric and oceanic conditions are currently changing in response to
50 increasing atmospheric concentrations of greenhouse gases and changes in the concentration of
51 stratospheric ozone (Swart et al, 2018). Model projections from the fifth phase of the Coupled
52 Model Intercomparison Project (CMIP5, Taylor et al., 2012) highlight a changing wind pattern
53 associated with a more persistent phase of the Southern Annular Mode (SAM), together with
54 warmer sea-surface temperature north of the sea-ice zone (Bracegirdle et al., 2013; Cai et al,
55 2003; Swart et al, 2015; Zheng et al, 2013). Such changes in the physical environment are
56 expected to affect the capacity of phytoplankton to fix atmospheric carbon, their community
57 composition and the overall efficiency of the biological carbon pump (Lenton and Matear, 2007;
58 Lovenduski and Gruber, 2005). In particular, it is critical to understand how physical changes
59 will alter iron and light availability, as these two elements play fundamental roles in structuring
60 the response of phytoplankton communities (Boyd et al, 2002).

61 In a recent review, Deppeler and Davidson (2017) identified a large number of factors able to
62 alter primary production in the Southern Ocean. Amongst these factors, changes in the seasonal
63 mixed-layer depth (MLD) were particularly important north of the sea-ice zone. However,
64 neither the sign nor the magnitude of change are yet clear due to the complex links between the
65 seasonal cycle of the MLD and primary production in the Southern Ocean. Two reasons
66 contribute to this complexity. First, the sign of the change in MLD is expected to vary regionally
67 and seasonally, depending on changes in surface warming, wind and freshwater fluxes (Panassa
68 et al, 2018, Sallée et al, 2013). Second, vertical mixing plays a complex role for phytoplankton,
69 since shallow MLDs may maintain cells in the well-lit part of the water column, but, at the same
70 time, the vertical extent of the upper mixing layer controls the vertical supply of iron from
71 deeper reserves. Thus, while a decrease in MLD enhances productivity in light limited conditions
72 through the first mechanism, it reduces productivity through the second mechanism in regions
73 where iron is supplied by vertical mixing in winter (Doney, 2006; Sarmiento et al, 2004). In this
74 second case, the winter supply of iron is more efficient when the mixed-layer deepens within the
75 subsurface iron reservoir (hereafter, we refer to the upper limit of the iron reservoir as the
76 ferricline, see methods for details). The two mechanisms described by this paradigm are
77 concomitant in the Southern Ocean, where both light limitation and iron limitation co-exist in

78 time and space (Boyd et al 2010). Moreover, given that such interplay varies throughout the
79 seasonal cycle, changes in the seasonal extremes of the MLD in winter and summer (MLD_{winter}
80 and MLD_{summer} , respectively) are expected to have different impacts on annual values of primary
81 production (Deppeler and Davidson, 2017, Hauck et al, 2015).

82 End-of-century projections from CMIP5 show a coherent latitudinal pattern of change in primary
83 production over the Southern Ocean (Bopp et al, 2013; Laufkötter et al, 2015). In the 30°-40°S
84 latitudinal band CMIP5 models agree on a nutrient-driven decrease in primary production as a
85 consequence of the broadening of oligotrophic gyres to southern waters (Hauck et al, 2015). In
86 the 40°-50°S latitudinal band, models project an increase in primary production, followed by a
87 decrease in the 50°-65°S band (Bopp et al 2013). Leung et al. (2015) found a consistent response
88 between models on the primary production increase at 40°-50°S. Their analysis associated the
89 change in primary production to a reduction of MLD_{summer} combined with an increase in surface
90 iron. Alternatively, the primary production decrease in the 50°-65°S band was not consistent
91 between models and has been linked to deeper MLD_{summer} combined with a reduction of the
92 incident photosynthetically available radiation. However, the mechanisms behind these changes
93 remain unclear as projected patterns have only been explained through correlation relationships
94 (Leung et al, 2015), or masked by the strong primary production increase associated to Antarctic
95 sea-ice decline (Laufkötter et al, 2015). The overlap between different drivers in climate models
96 does not allow evaluating the influence of changes in MLD alone over primary production.
97 Furthermore, the uncertainties in these models are likely to induce incorrect interpretations based
98 on theoretical paradigms (Lovenduski and Gruber, 2005). The largest uncertainty is caused by
99 the inability of CMIP5 models to correctly reproduce dissolved iron and MLD observations in
100 the Southern Ocean (Sallée et al, 2015; Tagliabue et al, 2016), particularly in winter. These
101 uncertainties cascade into the iron vertical supply and cause a model-dependent biogeochemical
102 response in the Southern Ocean (Schourup-Kristensen, 2014).

103 Moreover, the lack of mechanistic understanding and the uncertainties associated to primary
104 production drivers in the Southern Ocean also impact the estimates of how much carbon is
105 eventually transferred into the deep ocean. The export of carbon depends on a number of
106 processes such as the plankton community structure, remineralization rates, temperature or MLD
107 variability (Boyd and Trull, 2007; Henson et al, 2015). The disparities on how biogeochemical

108 models resolve these mechanisms add up to iron supply uncertainties and cause a lack of
109 agreement between climate-models in the Southern Ocean (Laufkötter et al, 2016). This lack of
110 consensus is particularly severe in the mid-latitudes, 44°-58°S (Hauck et al, 2015).

111 A number of observation-based studies provide evidences that in the Southern Ocean the two
112 aspects of the primary production-MLD paradigm (Fig 1 in Doney, 2006) might be occurring
113 simultaneously. Ardyna et al. (2017) combined data from satellite ocean-color with Argo floats
114 to show that regional variability in Southern Ocean phytoplankton biomass results from a mixed
115 balance of drivers in addition to light, including the proximity to island or submerged seamounts,
116 sea-ice, or MLD_{winter} . Interestingly, they show that, away from specific iron sources,
117 phytoplankton biomass increases as a function of MLD_{winter} , for MLD_{winter} ranging from 0 to
118 ~150m, but decreases for $MLD_{winter} > 150m$. They interpret the presence of such a regime shift
119 as a transition from an iron-limited environment (shallow MLD_{winter}) to a light-limited
120 environment (deep MLD_{winter}). Similarly, Hoppe et al. (2017) reported strong blooming
121 conditions in regions of deep mixing, suggesting a secondary role of light limitation on
122 controlling summer production. This result agrees with Venables and Moore (2010) who found
123 no influence of light limitation over the annual integrated chlorophyll-a in Southern Ocean
124 waters.

125 In this paper, we investigate how ongoing and future changes in winter and summer MLD may
126 influence primary production and the export of organic carbon with a modeling configuration
127 specifically designed to address this question in the context of the Southern Ocean. Our approach
128 avoids the complexity related to climate models and, at the same time, captures the double-role
129 of the MLD on primary production. To do so, we implemented a state-of-the-art biogeochemical
130 model into a fully controlled one-dimensional (1D) physical configuration. We varied MLD_{winter} ,
131 MLD_{summer} and ferricline depth (Z_{Fe}) along typical present and projected ranges for the Southern
132 Ocean. Despite the idealized approach, the statistical analysis of a large ensemble (752) of
133 simulated annual cycles showed a complex relationship between MLD, primary production and
134 export. Our results challenge current interpretations of CMIP5 projections in the Southern Ocean
135 and propose the presence of a threshold depth for MLD_{winter} below which production would
136 collapse.

137 2. Methods

138 Our model configuration represents an ocean water column resolved as a vertical grid of 75
139 equally spaced cells. Only vertical exchanges are considered (i.e., it is a 1D configuration). The
140 same configuration was used in Llorca et al. (2015) to study the bloom phenology in the SO and is
141 fully described therein; here we recall the fundamental model characteristics. We use the
142 biogeochemical model PISCES (Aumont and Bopp, 2006) that we force with three physical
143 variables: surface solar short-wave radiation, temperature and turbulent vertical mixing (κ_z).
144 These three variables are prescribed and follow a complete seasonal cycle starting on the 15th of
145 February. The vertical profile of κ_z is set as a step-like function, with a value of $1 \text{ m}^2 \text{ s}^{-1}$ within
146 an upper mixed-layer and a small open ocean mixing of $10^{-5} \text{ m}^2 \text{ s}^{-1}$ (Cisewski et al, 2005) below
147 the mixed-layer. The strong mixing in the upper layer ensures a homogenous vertical distribution
148 of phytoplankton and nutrients (Lévy, 2015). The depth of the surface mixed-layer (and thus the
149 penetration depth of strong vertical mixing) varies along an idealized seasonal cycle consisting
150 of three phases (Fig 1a,b): a first phase of linear deepening until the maximum depth ($\text{MLD}_{\text{winter}}$,
151 from 15th February to 15th September), a second phase of linear shoaling (from 15th September
152 to 15th December) and a period of constant depth in summer ($\text{MLD}_{\text{summer}}$, 15th December to 14th
153 February of the next year).

154 PISCES contains 24 biogeochemical tracers, among which five nutrients (nitrate, phosphate,
155 ammonium, iron, and silicate), two phytoplankton size classes (small and large) and two
156 zooplankton size classes (micro-zooplankton and meso-zooplankton). Large phytoplankton
157 differs from small phytoplankton by higher iron requirements and a greater iron half-saturation
158 constant.

159 Initial vertical profiles for macronutrient (i.e. nitrate, phosphate, and silicate) were constructed
160 based on the winter mean profiles of a typical HNLC region (Jeandel et al., 1998). We carried a
161 series of sensitivity experiments to ensure that only iron limits phytoplankton growth. The
162 summer initial condition for dissolved iron profile was constructed by assuming low
163 concentrations ($0.03 \text{ nmol Fe l}^{-1}$) above a prescribed depth and larger concentrations (0.5 nmol
164 Fe l^{-1}) below. The depth where iron concentration suddenly increases is referred here as the
165 ferricline (Z_{Fe}). Iron supply into the upper mixed layer is not prescribed, but emerges from the

166 vertical entrainment and diffusion of iron, which depends on the respective depth of the Z_{Fe} and
167 the MLD. While lateral advection might be another important source of dissolved iron in specific
168 SO regions, particularly in the lee of islands or continental shelves, it is neglected here to
169 concentrate on vertical entrainment of iron. Vertical entrainment of iron is likely the dominant
170 source of iron supply in most of the Southern Ocean, which is characterized by deep ferricline
171 (Tagliabue et al., 2014). In this study, iron supply is computed as the amount of dissolved iron
172 that enters MLD.

173 **Ensemble of runs**

174 The 1D physical setting forced the PISCES model under current and future MLD conditions. We
175 conducted an ensemble of simulations where we varied three forcing parameters, MLD_{winter} ,
176 MLD_{summer} (Pellichero et al, 2017) and Z_{Fe} (Tagliabue et al, 2014), over the full range of
177 observed values in the SO. Values for future MLD were obtained from CMIP5 climate model
178 projections (Sallée et al, 2013; Taylor et al, 2012). Overall, we prescribed 11 distinct values of
179 MLD_{winter} (between 100m and 600m), combined with 9 distinct values for MLD_{summer} (between
180 20m and 100m) and 8 Z_{Fe} values (between 150 and 500m). The combination of all MLD_{winter} ,
181 MLD_{summer} and Z_{Fe} values resulted in 752 different scenarios. This approach allowed us to
182 identify how changes in MLD affect primary production and export over a wide range of oceanic
183 conditions typical of the Southern Ocean.

184 **4 Results**

185 **4.1 Response to changes in winter MLD**

186 Southern Ocean open waters extend from mid to high-latitudes, with seasons being clearly
187 differentiated and incident Photosynthetically Available Radiation (PAR) being lower in winter
188 than in summer. However, the average light received by phytoplankton is lower than surface
189 PAR as cells are vertically mixed across the mixed-layer. The light used for the photosynthesis
190 can then be calculated using the PAR attenuation profile averaged across the mixed-layer
191 (PAR_{ML}). Thus, deeper (shallower) MLD_{winter} reduce (increase) PAR_{ML} , exacerbating (relaxing)
192 light limitation of phytoplankton growth and primary production (Boyd et al, 2010). MLD_{winter}
193 also has an impact on growth and primary production limitation by controlling vertical supply of

194 iron. Deeper MLD_{winter} tend to drive stronger iron supplies and enhance phytoplankton growth
195 (Tagliabue et al, 2014). We first examine how the combination of these two opposing
196 mechanisms (light and iron limitation) drive differences in primary production in three model
197 simulations that only differ by their MLD_{winter} values (deep, intermediate and shallow scenario),
198 with identical MLD_{summer} and Z_{Fe} (Fig 1, left panels).

199 From March to July, the seasonal decrease of surface PAR combined with the deepening of the
200 mixed-layer strongly decreased PAR_{ML} for all three scenarios (Fig 1a and b). PAR_{ML} remained
201 low until October, when the shoaling of the MLD caused a rapid increase (Fig. 1b). The vertical
202 supply of iron initiated when the mixed-layer depth crossed Z_{Fe} (Fig 1b). These two factors,
203 PAR_{ML} and iron supply, acted together to shape the response in primary production (Fig 1c and
204 d). From March to July, depth-integrated primary production was low and with a decreasing
205 trend (Fig 1c). For the three scenarios a period of slow increase started around July, and was
206 followed by a marked bloom in spring.

207 The three simulations exhibited differences in the timing and amplitude of the bloom (Fig. 1c).
208 In the shallow simulation, winter iron supply was relatively low ($24 \mu\text{molFe m}^{-2} \text{yr}^{-1}$) and the
209 bloom was the weakest and earliest. Production started increasing on July 1st and peaked in
210 November, shortly after the mixing layer started shoaling and a month after iron supply ceased
211 (Fig. 1a, b and c). On the contrary, the bloom in the deep MLD_{winter} simulation was the strongest
212 and the slowest to develop of all three scenarios. In this scenario, MLD_{winter} penetrated deeply
213 into Z_{Fe} , which enhanced the vertical flux of iron ($60 \mu\text{molFe m}^{-2} \text{yr}^{-1}$). Nevertheless, integrated
214 primary production did not increase until the mixed-layer started shoaling in October. The large
215 amount of accumulated iron during winter and the quick spring increase in PAR_{ML} supported a
216 strong, but relatively short bloom, peaking in December.

217 Interestingly, these two extreme simulations led to similar values of annual integrated primary
218 production ($74.8 \text{ gC m}^{-2} \text{yr}^{-1}$ for the shallow simulation and $75.5 \text{ gC m}^{-2} \text{yr}^{-1}$ for the deep
219 simulation, Fig 1d), yet the relative contributions of small and large phytoplankton were notably
220 different. The annual primary production supported by the large phytoplankton group
221 represented 34% of the total production for the iron-poor shallow simulation while for the iron-
222 rich deep simulation it reached 52% (dashed lines in Fig 1d).

223 When these two end-members simulations are compared to the intermediate MLD_{winter} scenario a
224 non-monotonic response of annual primary production to varying MLD_{winter} emerges. While the
225 bloom in the intermediate MLD_{winter} simulation presented intermediate characteristics (iron
226 supply was $53 \mu\text{molFe m}^{-2} \text{yr}^{-1}$, Fig 1c), it showed the highest annual production ($79.1 \text{ gC m}^{-2} \text{yr}^{-1}$)
227 of all three simulations (Fig 1d). The balance between a weak, long-lasting and small-
228 phytoplankton-dominated winter bloom; and a high, quick and large-phytoplankton-dominated
229 spring bloom appeared to be optimal in the case of the intermediate experiment.

230 When we analyzed the results from our ensemble of 752 simulations (Fig. 2a), two contrasted
231 modes emerged in the response of annual primary production (PP) to changes in MLD_{winter} . The
232 first mode was associated with a deep iron reservoir ($Z_{Fe} > 350 \text{ m}$), and the second mode with a
233 shallow iron reservoir ($Z_{Fe} < 250 \text{ m}$). Both modes presented non-monotonic PP- MLD_{winter}
234 relationships: for a given Z_{Fe} , PP increased as MLD_{winter} decreased, until MLD_{winter} reached a
235 threshold depth (Z_{PPmax} , indicated by the white contours in Fig. 2a), where the PP- MLD_{winter}
236 relationship reversed and PP started decreasing. The threshold depth marked a local maximum in
237 PP and depended on the Z_{Fe} mode. Situations with $250\text{m} < Z_{Fe} < 350\text{m}$ corresponded to a
238 transition regime between these two modes, characterized by the presence of two Z_{PPmax} (dashed
239 white lines in Fig. 2a).

240 The deep iron reservoir mode presented a relatively shallow Z_{PPmax} , at around 200 m. In this
241 mode, iron supplies were systemically low ($< 10 \mu\text{molFe m}^{-2} \text{yr}^{-1}$; black contours in Fig 2a), even
242 when MLD_{winter} was deeper than Z_{Fe} since on those occasions there was only a brief period
243 where MLD was deeper than Z_{Fe} . In contrast, the shallow Z_{Fe} mode was characterized by
244 relatively large iron supplies, which were proportional to MLD_{winter} . In this mode, the threshold
245 depths were deeper (between 350m and 500m) and depended strongly on Z_{Fe} .

246 In both modes, the iron supply and the contribution of the large phytoplankton group to total PP
247 responded monotonically to changes in MLD_{winter} . This highlights that, as for the example shown
248 in Fig. 1, the threshold depth of MLD_{winter} marks a boundary between two different community
249 responses: for MLD_{winter} shallower than Z_{PPmax} , the community is dominated by small-
250 phytoplankton, and PP of both large and small phytoplankton groups respond monotonically to
251 changes in iron supply (Fig 2b-c); for MLD_{winter} deeper than Z_{PPmax} , the community is dominated

252 by large-phytoplankton, and light becomes the dominant limiting factor, particularly for the
253 small-phytoplankton group (Fig 2b).

254 The role of zooplankton in these responses was also addressed by diagnosing the percentage of
255 PP grazed, hereinafter referred as the grazing efficiency. Our simulations show that grazing
256 efficiency was strongly dependent on the community structure (Fig 2d), as small phytoplankton
257 is more easily grazed than large phytoplankton. Such dependency suggests a minor role of
258 zooplankton grazing as it follows the change on community structure, which is in turn caused by
259 changes in MLD.

260 A further climate-relevant metric associated with marine production is how much of the organic
261 carbon synthesized in the upper ocean is exported to the deep ocean. Under shallow ferricline
262 conditions, the amount of production exported below 100m (EP) showed a non-monotonic
263 response to changing MLD_{winter} with a threshold depth at 500m (Fig. 3a). EP responded in
264 parallel to the productivity supported by the larger class of phytoplankton (Fig. 2c) because large
265 phytoplankton tends to aggregate and sink faster than small phytoplankton (Boyd and Trull,
266 2007; Laufkötter et al, 2016). In contrast, and unlike PP, under deep ferricline and small
267 phytoplankton conditions we observed a monotonic response, with a constant increase in export
268 as MLD_{winter} decreased (Fig 3a).

269 **4.2 Response to changes in Summer MLD**

270 Phytoplankton growth and primary production rates are the highest during late spring and early
271 summer as surface waters are replenished with iron and light is abundant (Boyd et al 2010).
272 Therefore changes in MLD_{summer} , even if small in magnitude, have the potential to influence
273 annual productivity (Laufkötter et al, 2015; Leung et al, 2015) and export (Hauck et al, 2015). In
274 order to understand the mechanisms by which changes in MLD_{summer} affect primary production,
275 we first compared three simulations with different values of MLD_{summer} (20, 50 and 80 meters)
276 but with, Z_{Fe} set to 150 meters and MLD_{winter} at 300m (Fig 1e). Dissolved iron supplies were
277 very similar among the three simulations but PAR_{ML} strongly differed, with values nine times
278 larger in the shallow experiment than in the deep one (Fig 1f). Stronger light limitation in the
279 deep experiment caused the bloom to be slightly weaker and last longer than in the shallow
280 experiment (Fig 1g). However, annual primary production was the largest in the deep experiment

281 and this mainly resulted from an increase of the productive volume which caused higher depth-
282 integrated primary production during summer (Fig 1h), despite having the lowest MLD-averaged
283 production rates, PP_{ML} (dashed lines in Fig 1h).

284 The decrease in annual primary production under shallower MLD_{summer} was consistent amongst
285 all 752 simulations (Fig. 2e). This response suggested that in our model annual primary
286 production was not light limited in summer. MLD_{summer} was always shallower than ferricline
287 depths and iron supply remained low for all scenarios (black lines in Fig 2 e, f, g). Export
288 production was less sensitive to changes in MLD_{summer} than primary production (Fig. 3b), due to
289 the larger contribution of small phytoplankton cells to productivity under deep MLD_{summer} (Fig.
290 2f).

291 **5 Discussion and Conclusions**

292 The analysis of our ensemble of model simulations revealed that changes in primary production
293 driven by changes in mixed-layer depth are more complex than previously thought. The change
294 in primary production in response to variations in winter mixed-layer was non-monotonous: total
295 primary production and winter mixed-layer depth were positively correlated for winter mixed-
296 layer depths above a certain threshold depth (that we refer as Z_{PPmax}), but negatively correlated
297 for winter mixed-layer depths below this threshold (Fig 2a). The Z_{PPmax} for the mixed-layer
298 emerged due to the overlap of the two limiting factors, light and iron availability (Fig 1b).
299 Interestingly, Z_{PPmax} was related to both the biogeochemical conditions and ecosystem
300 composition. For instance, Z_{PPmax} was shallower for iron-poor and small-phytoplankton
301 dominated conditions than for iron-rich conditions where the two phytoplankton groups
302 contributed more equally (Fig 2b). Our analysis also shown that, quite unexpectedly, deeper
303 summer mixed-layers induced larger total primary production, despite lower phytoplankton
304 growth rates, because of an increase in the productive water volume (Fig 1, right panels and Fig
305 2a). Lastly, our experiments contribute to an understanding of how changes in MLD can alter the
306 carbon export. As expected, phytoplankton size composition was crucial to controlling carbon
307 export (Fig 3a and b). Under conditions of deep winter mixed-layers and iron-rich environments,
308 decreasing the mixed-layer depth resulted in a reduction of the export by decreasing iron-supply
309 and the presence of fast-sinking large phytoplankton. However, this trend reversed within

310 environments dominated by small-phytoplankton and export increased with decreasing mixed-
311 layers. Two combined mechanisms likely controlled this trend. In the first place, a larger portion
312 of primary production was grazed by zooplankton (Fig 2d), hence more organic matter could be
313 exported as sinking particles in form of fecal pellets. In the second place, the shallower the
314 mixed-layer the easier for particles to escape from surface turbulence and sink into the ocean
315 (Pavelsky and Doney, 2018).

316 These results have consequences on how we understand current and future Southern Ocean
317 productivity and export. Firstly, because the iron distribution and winter mixed-layer in the
318 Southern Ocean are zonally asymmetric (Tagliabue et al, 2014), future trends in primary
319 production and export are also likely to vary in both latitude and longitude. This conclusion
320 agrees with the observed zonal asymmetries of phytoplankton phenology provinces (Ardyna et
321 al, 2017) and challenges the prevailing latitudinal pattern of primary production trends projected
322 by most CMIP5 models (Bopp et al, 2013, Leung et al, 2015). We conclude that the latter is
323 more likely to be caused by the inability of current climate models to correctly reproduce the
324 zonal asymmetries in MLD (Sallée et al, 2013) and iron distribution (Schourup-Kristensen, 2015,
325 Tagliabue et al, 2016). Secondly, the non-monotonic response of primary production to MLD
326 should be further explored, particularly in observations, in order to evaluate the threshold depth
327 in winter mixed-layer depth within contrasted bioregions and identify which ecosystems are
328 closer to collapse. Along this line, Ardyna et al. (2017) estimated an average threshold depth
329 over the whole Southern Ocean of ~150m (their Fig S2) that can be used as a benchmark for
330 future studies. From a modeling perspective, evaluating the evolution of trends by decade,
331 instead of just comparing two extreme decades (i.e. projected against historical) may help
332 elucidate the non-monotonic responses in CMIP projections. Lastly, summer results suggest that
333 changes in summer mixed-layer depth do not significantly affect iron supply because the
334 ferricline depth is always deeper than the deepest plausible range of climatological summer
335 mixed-layer depth (see Fig 1c in Tagliabue et al, 2014, which shows that the ferricline depth is
336 deeper than 200m over 75% of the observed summer iron profiles). Summer storms, however,
337 which have not been accounted for in this study, may be more effective in supplying iron in the
338 case of deeper summer mixed-layer depths (Carranza and Gille, 2015, Nicholson et al., 2016).

339 There are a number of assumptions in our modeling approach that should be kept in mind for
340 future comparisons against observations or more complex models. First, we did not account for
341 silicate limitation. The latter is the main limiting factor for diatoms during late summer in Sub-
342 Antarctic waters of the Southern Ocean (Leblanc et al, 2005). Changes in summer MLD might
343 have a role on re-supplying silicate and alter diatoms summer production. Second, the
344 biogeochemical model used here simulates iron remineralization in a simplistic way (Amount
345 and Bopp, 2006). In our analysis we did not detect any significant change in summer iron
346 concentration associated to remineralization. But it is possible that the representation of this
347 mechanism in our model is too simplistic, because remineralization has been identified as a
348 significant source of iron during summer in the Southern Ocean (Tagliabue et al, 2014 and
349 2017). How changes in summer mixed-layer depth influence remineralization is out of scope of
350 the current study but together with silicate limitation, these mechanisms could either compensate
351 or intensify the summer trends presented here. Third, we made the choice to not consider
352 changes in incoming solar radiation, and used clear-sky conditions at 45°S latitude in all our
353 experiments. At higher latitudes, where incoming solar radiation is lower, we would expect to
354 find shallower threshold depths, although this could be compensated by higher iron demand by
355 phytoplankton. More difficult is to anticipate the impacts of a non-clear-sky over phytoplankton
356 growth, as incoming solar radiation is simultaneously influenced by seasonal and intra-seasonal
357 variability of cloud coverage, typology of clouds (type and altitude in the atmosphere) and sea-
358 state (surface waves and bubbles). Fourth, we considered changes in MLD but we did not take
359 into account the associated changes in temperature and wind stress. The former is particularly
360 interesting, as laboratory experiments have recently shown interactive effects between iron and
361 temperature for Southern Ocean diatoms (Hutchins and Boyd, 2016). Last, our study is based on
362 a biogeochemical model that, despite its complexity, remains a simplification of the processes
363 regulating phytoplankton growth. For instance, community structure was only represented in
364 terms of size but it is well known that different phytoplankton species of similar sizes respond
365 differently to environmental changes (Arrigo et al., 1999). Also, our model did not account for
366 the potential contribution of vertically migrating zooplankton and small nekton to the carbon
367 export. We should note however that, despite these assumptions, the relationships between
368 primary production and MLD that came out of this modeling study are consistent with that

369 suggested from in-situ observations (Ardyna et al 2017, Hoppe et al 2017). Moreover, the
370 analysis of a large ensemble of simulations also supports the robustness of our conclusions.

371 In conclusion, the results presented here provide a new and more refined explanation of the
372 influence of MLD over Southern Ocean primary production and export. They provide a
373 framework to analyze current and future patterns of production and export, in particular for
374 CMIP6 projections and multiannual time-series obtained from *in-situ* observations such as
375 moorings or BGC-Argo floats.

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383 ensemble of model outputs used in this study can be freely accessed at:
384 <https://metadata.imas.utas.edu.au/geonetwork/srv/eng/main.home> ; and the PISCES code specific
385 for the model configuration used in this study is available at <https://github.com/jllort>.

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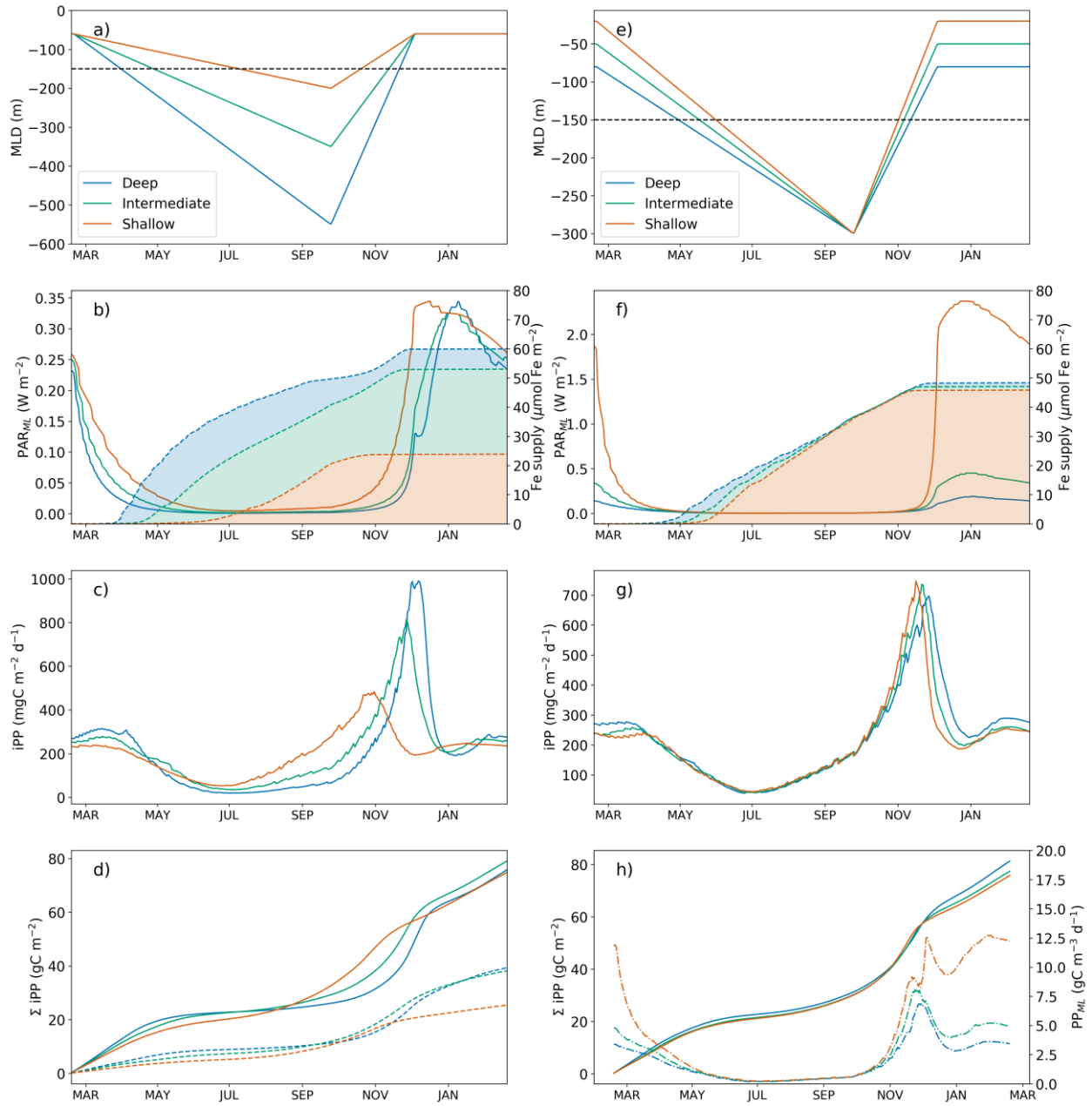
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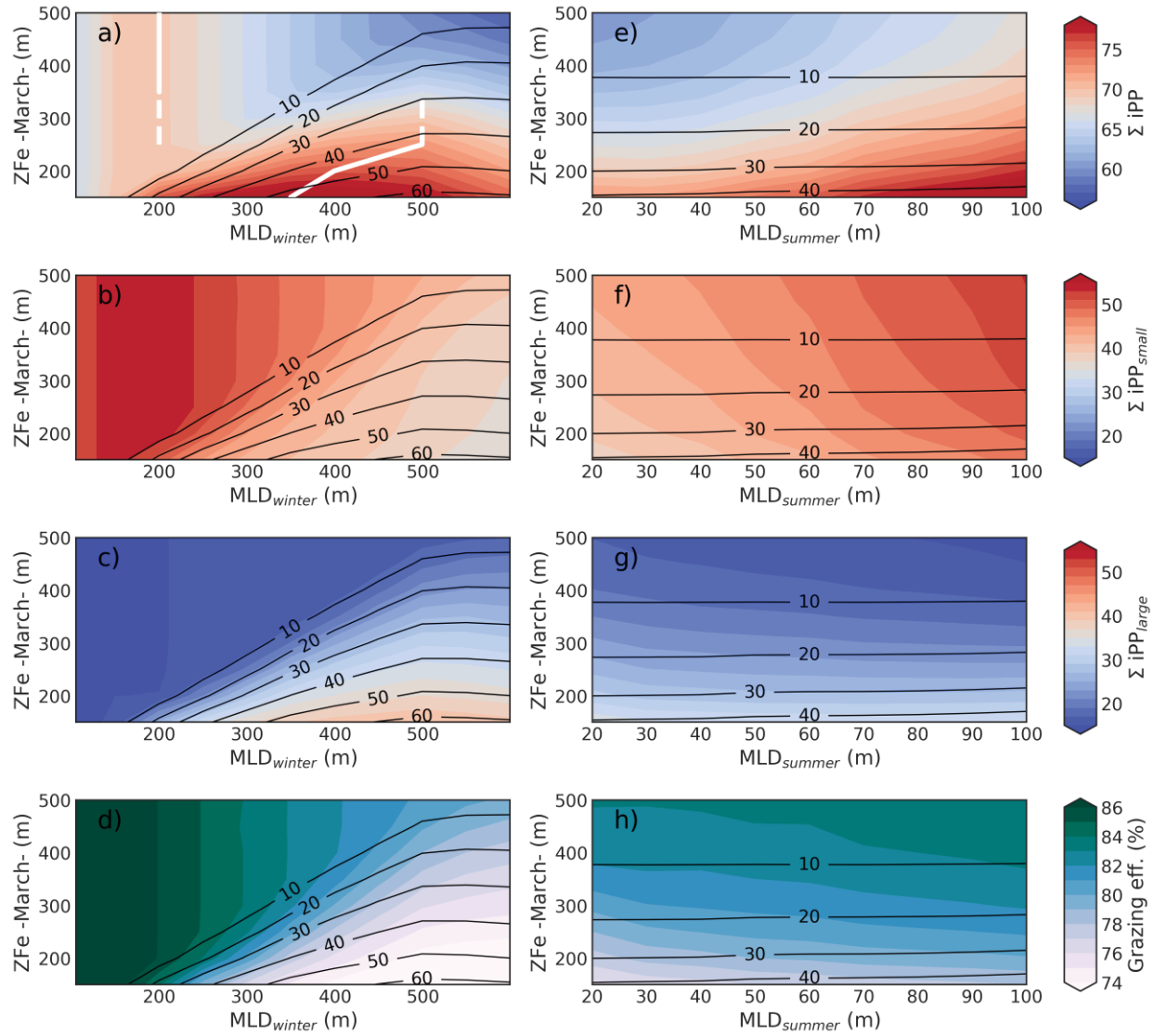
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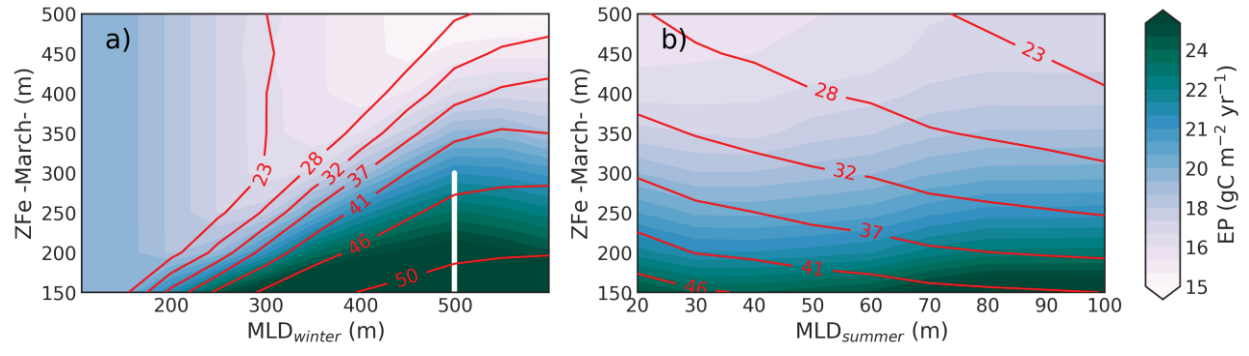
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524 CAPTIONS

525 **Figure 1:** Left panels: Seasonal cycles of (a) mixed layer depth, (b) averaged PAR in the MLD (plain lines) and
526 time-cumulative vertical supply of iron (dashed contours with colors filled) into the MLD, (c) depth-integrated
527 primary production (iPP), and (d) time-cumulative integrated primary production (Σ iPP, plain lines) and integrated
528 primary production for the large-phytoplankton group (dashed lines) for three simulations with identical Z_{Fe} depth
529 and MLD_{summer} but with different MLD_{winter} . The black dashed line in (a) indicates the value of Z_{Fe} . Right panels:
530 same but for simulations runs with identical Z_{Fe} depth and MLD_{winter} and different MLD_{summer} . In h), dash-dotted
531 lines represent primary production averaged in the mixed-layer (PP_{ML}).

532 **Figure 2:** Left panels: a) Annual integrated Primary Production (in $gC\ m^{-2}\ yr^{-1}$) as a function of initial Ferricline
533 depth (Z_{Fe}) and winter MLD (MLD_{winter}). White solid lines indicate threshold depths (Z_{PPmax}) and white dashed lines
534 indicate the range where two different thresholds were detected. c) Same as a) but for small phytoplankton. c) Same
535 as a) but for large phytoplankton. d) Portion of annual primary production grazed by zooplankton (grazing
536 efficiency). In all panels, the black contours show the vertical supply of iron ($nmolFe/yr$). Right panels: same, but
537 against summer MLD (MLD_{summer}).

538 **Figure 3:** a) Annual Primary Production exported below 100m depth as a function of initial Ferricline depth (Z_{Fe})
539 and winter MLD (MLD_{winter}). Red contours show the percentage of primary production done by the large (and fast-
540 sinking) phytoplankton. The white line indicates the threshold depth for EP-MLD relationship. b) Same as a) but
541 against summer MLD (MLD_{summer}).

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Figure 1.

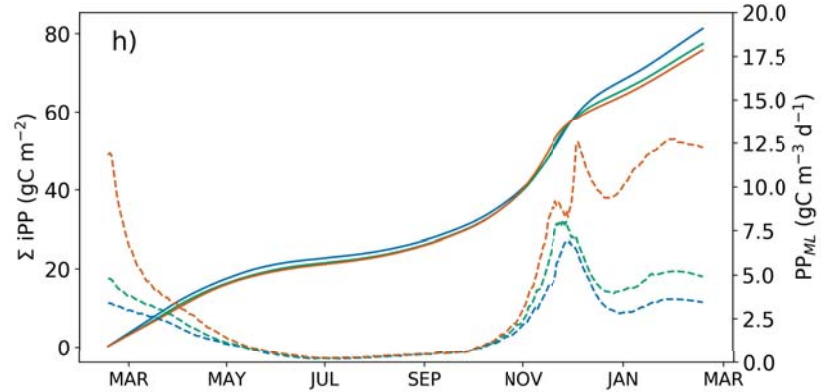
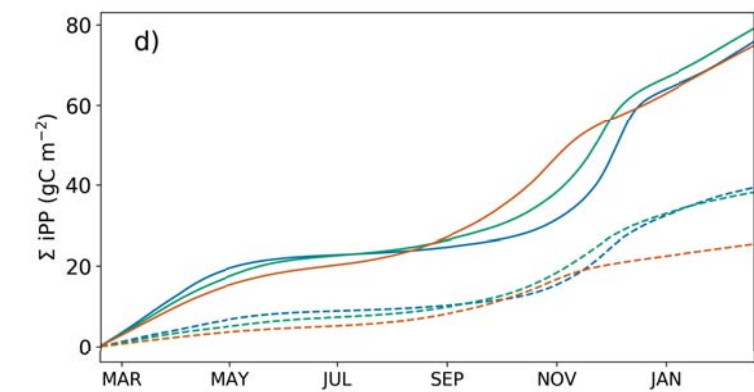
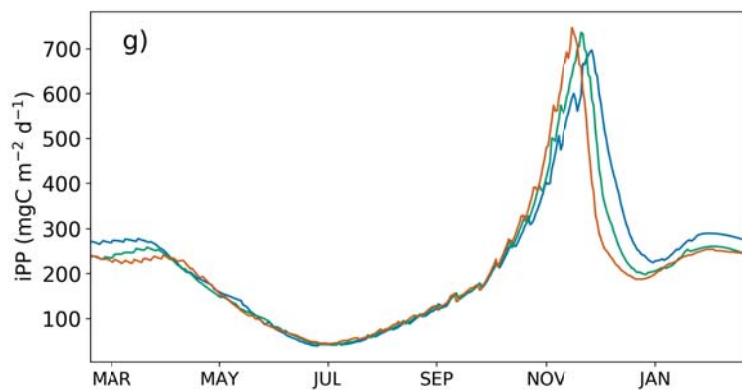
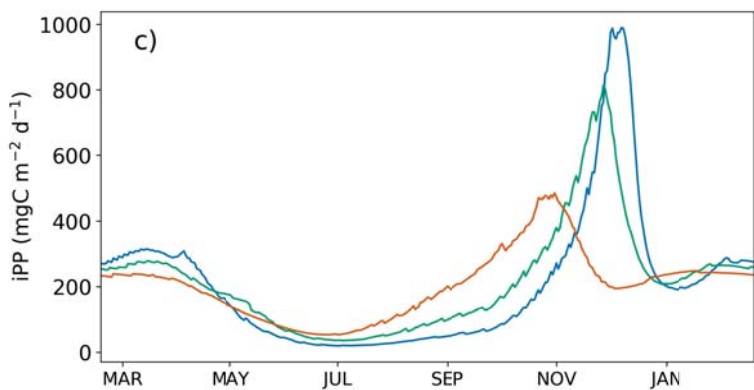
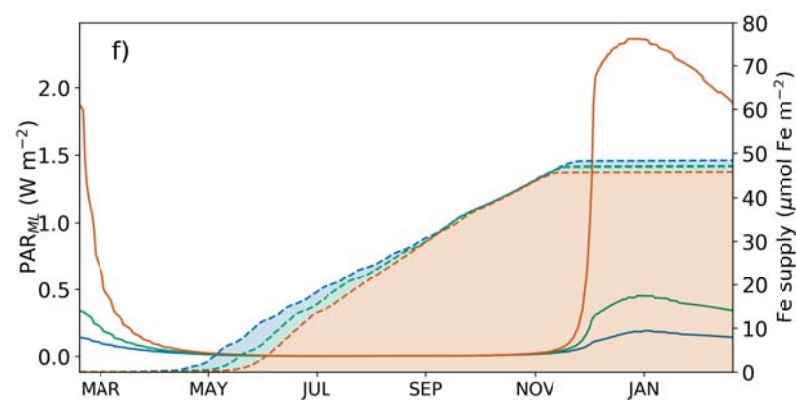
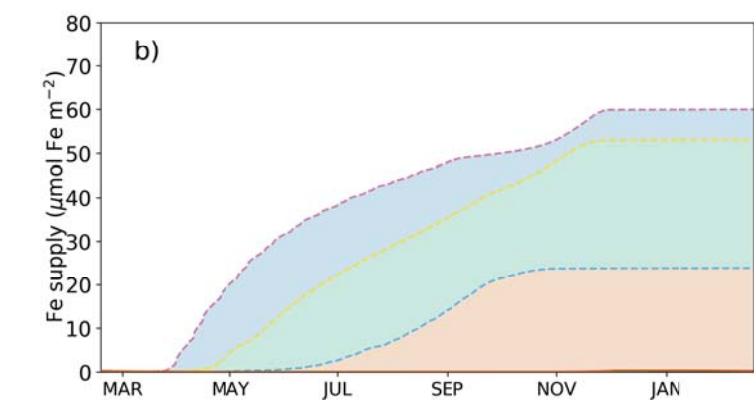
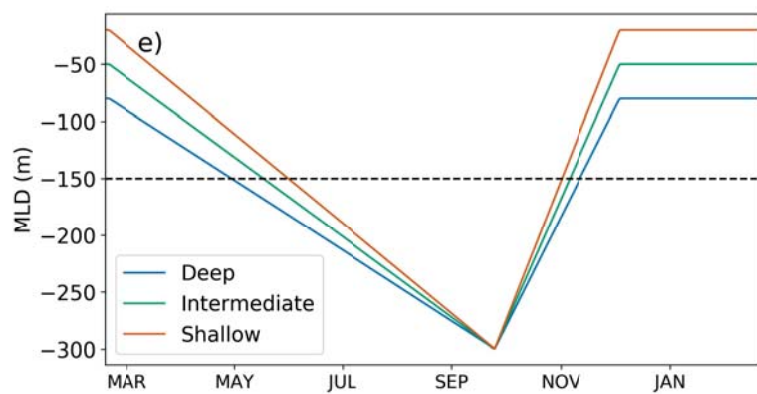
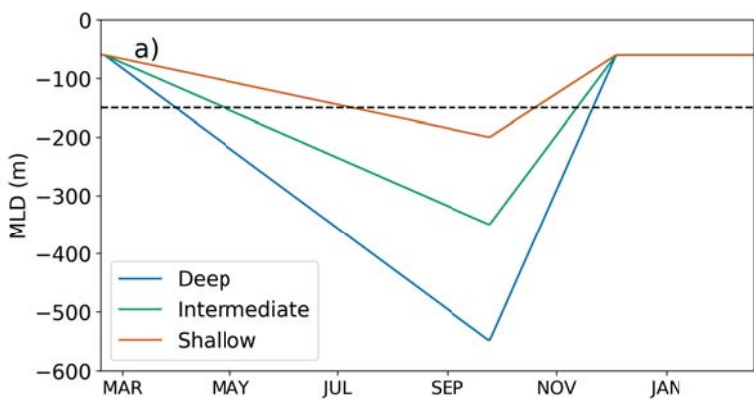


Figure 2.

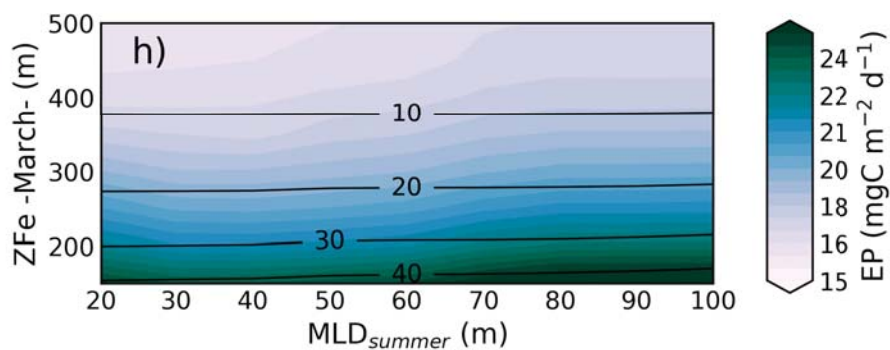
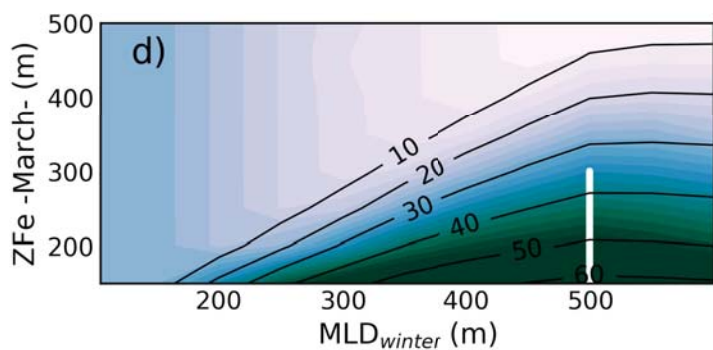
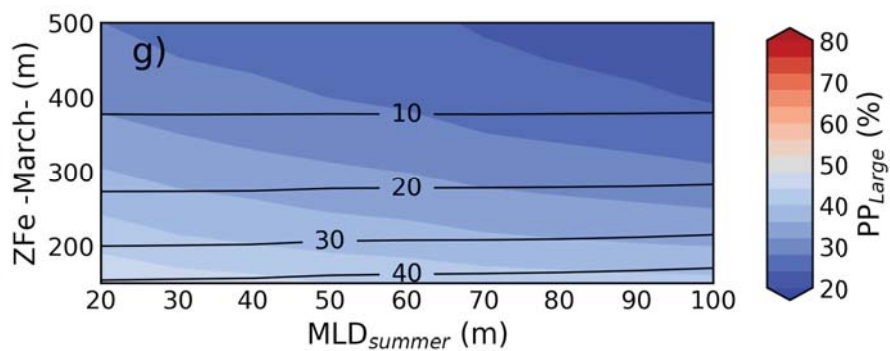
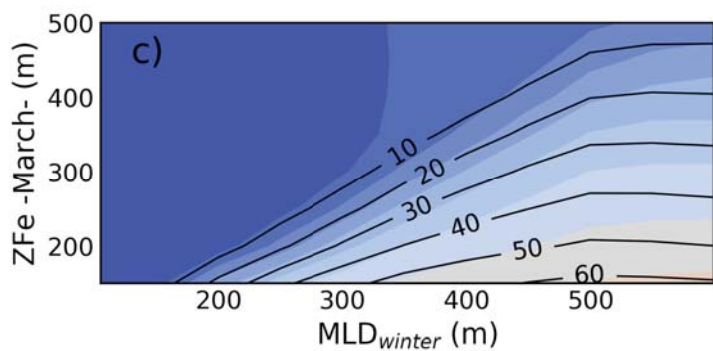
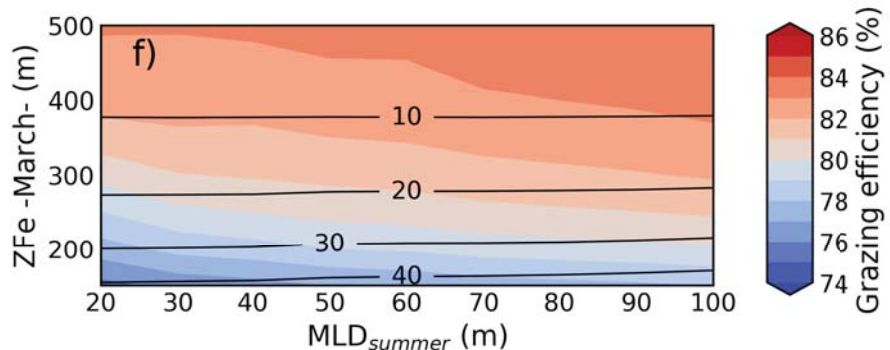
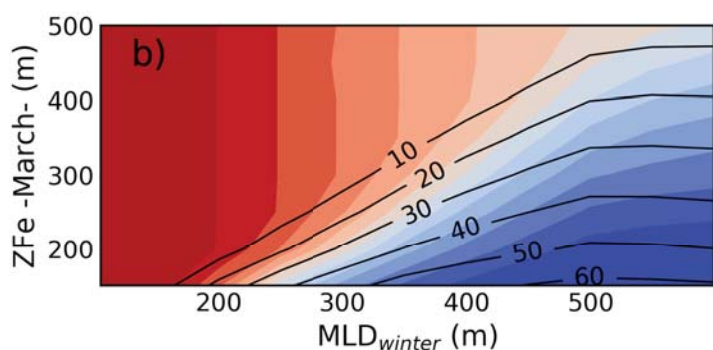
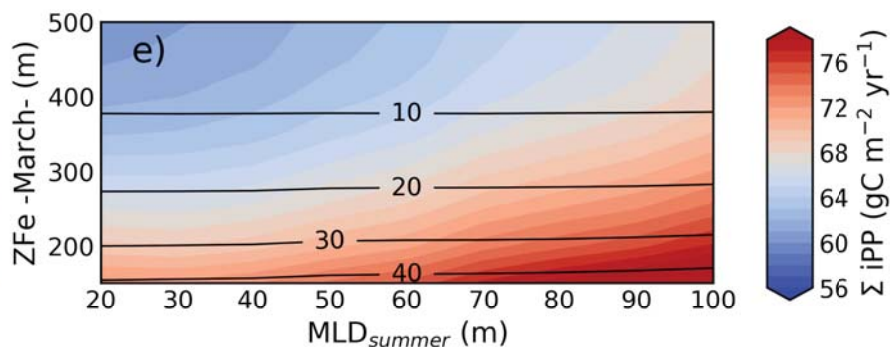
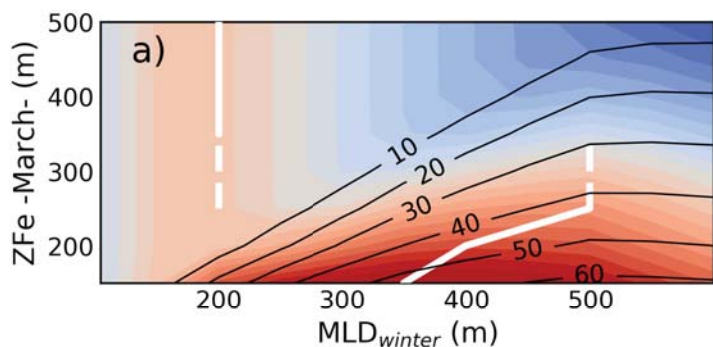


Figure 3.

