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1 Meridional contrasts in productivity changes driven by the opening of

2 Drake Passage

3

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16

## 17 **Keypoints**

18 • Productivity changes following Drake Passage opening are explored using the IPSL model  
19 and compared with data from the late Eocene and early Oligocene.

20 • Drake Passage opening drives a decrease in productivity in the low latitudes and spatially  
21 heterogeneous patterns in the high latitudes.

22 • Agreement between proxy records and model results indicate that Drake Passage opening  
23 has driven part of the late Eocene productivity changes.

24

25 **Abstract**

26 Changes in atmospheric pCO<sub>2</sub> are widely suggested to have played a major role in both the  
27 long-term deterioration of Cenozoic climate and many superimposed rapid climate  
28 perturbations such as the pivotal Eocene-Oligocene transition. Changes in marine productivity  
29 affecting the biological oceanic carbon pump represent one possible cause of past CO<sub>2</sub>  
30 variability. Here, we explore the relationship between ocean gateway change and marine  
31 biogeochemistry. Specifically, we use a fully coupled atmosphere-ocean-biogeochemical  
32 model (IPSL-CM5A) to examine global ocean paleoproductivity changes in response to the  
33 opening of Drake Passage. In our simulations, we find that Drake Passage opening yields a  
34 spatially uniform decrease in primary productivity in the low latitude oceans while the high  
35 latitude response is more spatially heterogeneous. Mechanistically, the low latitude  
36 productivity decrease is a consequence of a fundamental reorganization of ocean circulation  
37 when Drake Passage opens driven by the isolation of the Southern Ocean from low latitude  
38 water masses. Nutrient-depletion in the low latitudes is driven by a marked decrease in the  
39 intensity of deep convection in the Southern Ocean, which drives the accumulation of  
40 nutrients at depth and their depletion in the intermediate and upper ocean, especially away  
41 from sites of subduction. In the high latitudes, the onset of the Antarctic Circumpolar Current  
42 in the model exerts a strong control both on nutrient availability but also on regions of deep-  
43 water formation. The qualitative agreement between geographically diverse long-term  
44 paleoproductivity records and the simulated variations suggests that Drake Passage opening  
45 may contribute to the long-term paleoproductivity signal.

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49

## 50 **Introduction**

51 Tectonic opening of Southern Ocean gateways constitutes one of the most  
52 fundamental changes in Cenozoic boundary conditions because of the capacity to alter global  
53 ocean circulation and climate [*Barker and Burrell, 1977; Kennett, 1977*]. In a seminal paper,  
54 *Kennett [1977]* proposed that the opening of these gateways (Drake and Tasman Passages) to  
55 deep circulation was instrumental in initiating sustained Antarctic glaciation. This sequence of  
56 events is suggested to have initiated during the late Eocene [*Matthews and Poore, 1980;*  
57 *Miller et al., 1991; Lear et al., 2000; Stickley et al., 2004; Lagabrielle et al., 2009*], although  
58 debate is ongoing about the timing of full gateway opening to a deep and wide current system  
59 [*Barker et al., 2007; Katz et al., 2011; Scher et al., 2015*]. This appealing hypothesis suggests  
60 that the opening of Drake Passage (DP) and of the Tasman gateway would have engendered  
61 the onset of an Antarctic Circumpolar Current (ACC), thermally isolating the Antarctic  
62 continent from water masses sourced in the lower latitudes and permitting the growth of an  
63 extensive Antarctic ice sheet (AIS). However, this ocean gateway hypothesis has  
64 subsequently lost some ground because the results of numerical model experiments have been  
65 unable to robustly demonstrate that the sole climatic impact of DP (or Tasman gateway)  
66 opening was sufficient to initiate the glaciation [*Mikolajewicz et al., 1993; DeConto and*  
67 *Pollard, 2003; Huber and Nof, 2006; Sijp et al., 2011; Goldner et al., 2014*]. Instead,  
68 modelling studies have pointed to a CO<sub>2</sub> decline as the primary driver of AIS initiation  
69 through atmospheric radiative cooling [*Mikolajewicz et al., 1993; DeConto and Pollard,*  
70 *2003; Huber et al., 2004*]. The remarkable match between observations [*Coxall et al., 2005;*  
71 *Coxall and Wilson, 2011*] and model predictions [*DeConto and Pollard, 2003; Ladant et al.,*  
72 *2014*] of the structure of the deep sea oxygen isotope record across the Eocene-Oligocene  
73 transition (EOT) and paleo-CO<sub>2</sub> reconstructions for this interval [*Pearson et al., 2009; Pagani*  
74 *et al., 2011; Heurreux and Rickaby, 2015*] lend support to the CO<sub>2</sub> hypothesis. Yet these CO<sub>2</sub>

75 reconstructions are far from well-developed and the influence of ocean gateway opening and  
76 CO<sub>2</sub> forcing need not be mutually exclusive [*Egan et al.*, 2013; *Lear and Lunt*, 2016;  
77 *Elsworth et al.*, 2017].

78         There exists a rich literature documenting long-term changes in oceanic carbon  
79 cycling associated with Cenozoic climate deterioration including across the pivotal EOT  
80 thanks to scientific ocean drilling [e.g., *Siesser*, 1995; *Schumacher and Lazarus*, 2004; *Faul*  
81 *and Delaney*, 2010; *Griffith et al.*, 2010; *Coxall and Wilson*, 2011; *Pälike et al.*, 2012; *Egan*  
82 *et al.*, 2013; *Moore et al.*, 2014; *Plancq et al.*, 2014; *Villa et al.*, 2014]. Paleoproductivity  
83 reconstructions from the data – taken here to mean export production of organic matter to the  
84 deep ocean since most paleo data studies inherently quantify export production rather than  
85 primary productivity – display spatially heterogeneous long-term variations between the late  
86 Eocene and the Oligocene (Table 1). Data from the northern high-latitudes are lacking but  
87 records from the southern high-latitudes generally document paleoproductivity increases from  
88 the Eocene into the Oligocene [*Schumacher and Lazarus*, 2004; *Plancq et al.*, 2014; *Villa et*  
89 *al.*, 2014] while the low latitudes record a general decrease [*Schumacher and Lazarus*, 2004;  
90 *Griffith et al.*, 2010; *Moore et al.*, 2014].

91         Numerical modelling studies have investigated the role of DP opening on global ocean  
92 circulation and climate with spatially resolved Earth system models [*Mikolajewicz et al.*,  
93 1993; *Toggweiler and Bjornsson*, 2000; *Sijp and England*, 2004; *Sijp et al.*, 2009; *Zhang et*  
94 *al.*, 2010; *Sijp et al.*, 2011; *Yang et al.*, 2014; *Fyke et al.*, 2015; *England et al.*, 2017]. In  
95 contrast, modelling of ocean biogeochemical changes across the late Eocene and Oligocene  
96 has been limited. Most work of this type has been undertaken using either numerical box  
97 models focusing specifically on the Eocene-Oligocene Transition itself [*Zachos and Kump*,  
98 2005; *Merico et al.*, 2008; *Armstrong McKay et al.*, 2016] or using the UVic earth system  
99 model of intermediate complexity (EMIC) integrating a biogeochemical component [*Pagani*

100 *et al.*, 2011; *Fyke et al.*, 2015]. Box models are powerful tools to investigate the credibility of  
101 competing hypotheses at the global scale but they cannot be used to confront localized  
102 paleoproductivity reconstructions. On the other hand, results from experiments using the  
103 UVic EMIC suggest that the successive opening of DP and of the Panama seaway through  
104 Cenozoic time would have exerted a major influence on the inter-basin carbon reservoir and  
105 in setting the modern dissolved inorganic carbon gradients between basins [*Fyke et al.*, 2015].  
106 *Pagani et al.* [2011] utilize an Eocene UVic simulation to generate Eocene-Oligocene surface  
107 ocean phosphate concentrations, which they further use to compute surface ocean CO<sub>2</sub>  
108 concentrations to ultimately constrain their reconstructions of atmospheric CO<sub>2</sub> across the  
109 EOT. Their results also suggest that, compared to modern, the surface ocean phosphate  
110 concentration increases in the low latitudes and decreases in the high latitudes.

111         Here, we revisit the question of the biogeochemical impacts of DP using a more  
112 sophisticated, fully coupled, IPCC-class model with, for the first time, a focus on  
113 paleoproductivity changes and we compare our results with long-term records of productivity  
114 change from the late Eocene to Oligocene. It should be noted that *Winguth et al.* [2012] also  
115 applied a fully-coupled IPCC-class GCM to investigate paleoproductivity changes during the  
116 Eocene, but their focus was the PETM and as such they realized simulations at different CO<sub>2</sub>  
117 rather than with open or closed gateways. Assessing the role DP opening played in driving  
118 paleoproductivity changes during the late Eocene and Oligocene is important because of its  
119 influence on the global carbon cycle and in particular pCO<sub>2</sub> variations, via changes in the  
120 oceanic biological pump (see *Hain et al.* [2014] for a review). In the following, we explore  
121 the effects of opening DP on long-term productivity changes using a similar approach to that  
122 of *Fyke et al.* [2015] and *Elsworth et al.* [2017] in that we employ continental and  
123 bathymetric configurations altered from those of present-day. In this respect, strictly speaking,  
124 our experiment is a paleogeography sensitivity simulation rather than a simulation of Eocene-

125 Oligocene events. Nevertheless, our approach allows us to isolate the effect of DP opening on  
126 global climate and productivity and to make a semi-quantitative comparison to proxy records.  
127 Here we focus on comparing our results to records spanning the late Eocene and early  
128 Oligocene – the canonical interval for which DP opening is invoked as a climate forcing  
129 mechanism – but the possibility that a fully developed ACC was only established during the  
130 late Miocene [e.g., *Dalziel et al.*, 2013] also lends our results a longer-term Cenozoic  
131 relevance.

132

### 133 **Models**

134 The results presented in this study are obtained with the IPSL-CM5A Earth System  
135 Model [*Dufresne et al.*, 2013], which includes both a representation of the physical  
136 atmosphere-ocean-land-sea ice interactions and of the global carbon cycle. Its configuration  
137 combines the atmospheric model LMDz [*Hourdin et al.*, 2013], the land-surface model  
138 ORCHIDEE [*Krinner et al.*, 2005] and the ocean model NEMOv3.2 [*Madec*, 2008]. The  
139 OASIS coupler [*Valcke*, 2006] is used to interpolate and exchange variables and synchronize  
140 the models [*Dufresne et al.*, 2013]. Only succinct details about the models will be given here  
141 because their full description can be found in *Dufresne et al.* [2013] (see also *Kageyama et al.*  
142 [2013] for a description of the model used in paleo configurations for the Last Glacial  
143 Maximum and the mid-Holocene). LMDz solves the equation of atmospheric motion on a  
144 regular longitude-latitude grid using  $\sigma$ -P vertical coordinates. The resolution used in this  
145 study is 96x95x39 (lon. x lat. x vert.), corresponding to 3.75° of longitude and 1.875° of  
146 latitude, and 39 vertical levels irregularly distributed. ORCHIDEE runs on the same grid as  
147 LMDz and contains a land-surface scheme that simulates both the energy and water cycles of  
148 soils and vegetation and a routing scheme that routes precipitated water to the ocean. 12 Plant  
149 Functional Types (PFT) define the vegetation. Although the vegetation cover is imposed in



150 this version of IPSL-CM5A, the PFT phenology is computed interactively given the  
151 atmospheric state simulated by LMDz. The NEMO model comprises an ocean dynamics  
152 component (OPA, *Madec* [2008]), a thermodynamic-dynamic sea-ice model (LIM2, *Fichefet*  
153 *and Morales Maqueda* [1997]), and an ocean biogeochemistry model (PISCES, *Aumont and*  
154 *Bopp* [2006]). NEMO uses a tripolar grid in order to avoid North Pole singularity [*Madec and*  
155 *Imbard*, 1996], for both dynamics and physics. It has a nominal latitudinal resolution of 2°,  
156 increasing up to 0.5° at the Equator, and a longitudinal resolution of approximately 2° and 31  
157 unequally spaced vertical levels, the thickness of which varies from 10 m near the surface to  
158 500 m at the bottom. PISCES includes a simple representation of the marine ecosystem and of  
159 the main oceanic biogeochemical cycles [*Aumont and Bopp*, 2006]. It explicitly represents  
160 two classes of phytoplankton (nanophytoplankton and diatoms), two classes of zooplankton,  
161 five pools of nutrients (phosphate, nitrate, silicic acid, ammonium and iron), two classes of  
162 particulate organic carbon (small and large) and semi-labile dissolved organic carbon. It also  
163 includes dissolved and particulate inorganic carbon, alkalinity and dissolved oxygen. The  
164 main biogeochemical interactions, such as photosynthesis, respiration, grazing, particle  
165 aggregation and sinking, and remineralization, dictate the spatio-temporal evolution of each  
166 pool with respect to each other. Phytoplankton growth is limited by the aforementioned  
167 nutrients and by light availability. Ratios of C:N:P in the organic pools are kept constant  
168 following *Takahashi et al.* [1985], whereas Fe:C ratios for both phytoplankton classes and  
169 Si:C ratios for diatoms are prognostically simulated as a function of the external concentration  
170 of nutrients and light availability [*Aumont and Bopp*, 2006]. The full description of the  
171 version of PISCES used in this study can be found in *Aumont and Bopp* [2006]. All these  
172 models have been validated and used, either separately or together within the IPSL-CM5A  
173 model, over a variety of climates that include pre-Quaternary climates [e.g., *Contoux et al.*,  
174 2015; *Tan et al.*, 2017], LGM [e.g., *Mariotti et al.*, 2012; *Kageyama et al.*, 2013],

175 preindustrial [*Le Mézo et al.*, 2017] and present-day and future climates [e.g., *Aumont and*  
176 *Bopp*, 2006; *Bopp et al.*, 2013; *Tagliabue et al.*, 2014], including the latest IPCC exercise.

177 In a first step, two simulations are run with the fully coupled IPSL-CM5A model.  
178 Both simulations have a preindustrial land-sea mask, from which the geometry of the Panama  
179 Seaway has been altered to represent mid-Cenozoic tectonic configurations (in practice, this  
180 means replacing continental grid points by oceanic grid points, see Supplementary Fig. 1). In  
181 addition, the land-sea mask of the first simulation, named DC (for Drake Closed), has been  
182 modified to add terrestrial points at the Drake Passage to simulate its closure. Conversely, the  
183 Drake Passage is left unchanged from that of the preindustrial in the land-sea mask of the  
184 second simulation, named DO (Drake Opened). Compared to preindustrial conditions, ice  
185 sheets over polar continents have been removed and replaced by tundra-like vegetation but  
186 otherwise the preindustrial vegetation cover is kept for both simulations. The ocean is  
187 initialized as homogeneous in salinity ( $34.5 \text{ kg.m}^{-3}$ ) and with surface temperature following a  
188 latitudinal profile ranging from  $9^{\circ}\text{C}$  at the poles to  $36^{\circ}\text{C}$  at the equator. The deep ocean is  
189 initialized at a uniform temperature of  $7^{\circ}\text{C}$  (Supplementary Fig. 2). There is no sea ice at the  
190 beginning of the simulations. We prescribe a  $\text{CO}_2$  concentration of 1120 ppm, which is  
191 consistent with most of the records of paleo- $\text{CO}_2$  levels for the Eocene [*Berling and Royer*,  
192 2011] and justifies the absence of ice sheets over the poles because the inception of ice over  
193 Antarctica is thought to occur at lower  $\text{CO}_2$  levels [*Gasson et al.*, 2014; *Ladant et al.*, 2014;  
194 *Heureux and Rickaby*, 2015]. Each of the two experiments is run for 1000 years. We  
195 acknowledge here that longer integrations ( $\geq 3000$  years) are desirable but we are precluded  
196 by the computational performances of this version of the IPSL-CM5A model. However, after  
197 1000 years, the surface ocean is in equilibrium and the very small residual trend ( $< 0.1$   
198  $^{\circ}\text{C}/\text{century}$ ) that exists in the deep ocean is unlikely to significantly affect the outcomes of the  
199 study.

200 Oceanic biogeochemical equilibrium typically requires longer simulations to be  
201 attained than the dynamical equilibrium [S  ferian *et al.*, 2016]. In a second step, we run  
202 offline simulations of the PISCES model in order to be closer to the biogeochemical  
203 equilibrium. PISCES is initialized with the oceanic biogeochemical outputs from the last year  
204 of DC and DO coupled experiments and forced by the ocean dynamical fields of DC and DO.  
205 In detail, the last 100 years of ocean dynamics outputs are passed to PISCES-offline in a  
206 repetitive sequence (that is, after each 100 years of simulation, the ocean forcing is repeated  
207 for the next 100 years). The simulations DC-P (for DC-PISCES) and DO-P are run for 2000  
208 years to ensure equilibrium of the biogeochemical fields. One caveat must be noted here. In  
209 this version of IPSL-CM5A, the nutrient delivery to the ocean is fixed. This is an important  
210 simplification because under different climates the global amount of nutrients as well as the  
211 spatial distribution of nutrient inputs to the ocean (i.e., the intensity and location of the river  
212 flows) will be altered. However, as our purpose is to isolate the climatic and biogeochemical  
213 effects of DP opening only and to provide insights into its long-term signature in the proxy  
214 record, we have kept present-day nutrient inputs in the simulations.

215 In the following, we refer to the closed (open) Drake Passage simulations by DC (DO)  
216 regardless of whether we consider the fully coupled IPSLCM5A or the PISCES-offline  
217 simulation, but dynamical results utilize the IPSLCM5A simulations while the  
218 biogeochemistry is discussed using the PISCES-offline simulations.

219

## 220 **Results**

221 In the simulations, the opening of DP significantly alters paleoproductivity (i.e., paleo  
222 export production). Figure 1 shows the DC and DO global annual export production of  
223 organic carbon at 100 m, a commonly used measure of the carbon export into the deep ocean.  
224 The major areas contributing to this export are similar in the two simulations (Fig. 1) but in

225 regions such as the low latitude Indian and Pacific oceans, productivity uniformly decreases  
226 with DP opening (Figs. 1 and 2). In contrast, in the Southern Ocean, while productivity  
227 decreases in the Atlantic sector, it increases in the Pacific and Indian sectors when DP opens.  
228 In the zonal average, opening DP yields an increase in carbon export to the deep ocean in the  
229 southern high latitudes but a decrease in the low latitudes and northern high latitudes. This  
230 dipole pattern of increase in the southern high latitudes and decrease in the low latitudes  
231 agrees with the meridional contrast seen in the data (Table 1). The spatial pattern of  
232 increase/decrease in our simulations also compares favourably with observations from various  
233 drilling locations (Fig. 1).

234         The observed patterns of paleoproductivity change are the consequence of alterations  
235 in ocean circulation, which controls the supply of nutrients, essentially nitrate and phosphate,  
236 brought from the deep or sub-surface ocean to the surface. The zonally averaged  
237 redistribution of nutrients follows a dipole pattern on the vertical (Fig. 3) with a decrease in  
238 the intermediate and upper ocean and an increase at depth when DP opens, except in the  
239 highest latitudes of the Southern Ocean ( $> 60^{\circ}\text{S}$ ). Indeed, in this region, an increase in the  
240 concentration of nutrients occurs throughout the whole water column when DP opens.  
241 Vertical gradients in the upper 500 m confirm the decreased nutrient availability in the low  
242 latitudes of each basin in DC and the increase in the southern high latitudes (Fig. 4), except in  
243 the upper 100 m of the Atlantic sector.

244         The redistribution of nutrients in our simulations directly follows the reorganization of  
245 the oceanic thermohaline circulation (Figs. 5 and 6). In DC, the circulation is dominated by a  
246 vigorous Southern Hemisphere overturning cell of up to 30 Sv (Fig. 5), which is fed via deep  
247 convection ( $> 2000$  m) in the Pacific and Atlantic sectors of the Southern Ocean (Fig. 6).  
248 These deep waters then fill the deep ocean globally, circulate northward in the abyss, are  
249 strongly upwelled in the low latitudes at depth and return southward between 500 m and 1500

250 m depth. There is no deep-water formation in the Northern Hemisphere and the closed DP  
251 prevents the existence of a well-developed ACC. A wind-driven circumpolar circulation still  
252 develops around Antarctica under the influence of the Westerlies (Supplementary Fig. 3),  
253 which generates upwelling cells carrying waters from the southward branch of the overturning  
254 circulation to the surface. Some of these waters then feed the abyssal circulation through deep  
255 convection around Antarctica while the remaining fraction is advected northward to feed  
256 intermediate and modal ocean circulation [Toggweiler and Samuels, 1993]. The absence of a  
257 well-developed ACC leads to enhanced export of warm and salty subtropical waters into the  
258 Southern Ocean, increasing the intensity of deep water formation there as well as the  
259 southward ocean heat transport [Sijp and England, 2004].

260         Opening DP strongly modifies the global ocean circulation (Fig. 5). Arguably, the  
261 major difference lies in the appearance of a vigorous modern-like ACC (Supplementary Fig.  
262 3), which interconnects the three major basins from top to bottom and generates a relatively  
263 deep Deacon Cell (~ 2000 m), which reflects the existence of deep upwelling cells. The latter  
264 are deeper and more expanded towards Antarctica relative to DC, as shown by the overlain  
265 isopycnals on Figs. 3a and 3b, and then feed the abyssal and the intermediate/modal  
266 circulations as in DC. Abyssal waters formed around Antarctica remain however mostly  
267 confined below 2000 m (Fig. 5). The existence of a well-developed ACC limits the advection  
268 of warm and salty subtropical waters to the Southern Ocean, which reduces the intensity of  
269 deep convection (Fig. 6) because at high latitudes, salinity exerts the dominant control over  
270 the stratification of ocean waters [Ferreira *et al.*, 2010; Yang *et al.*, 2014]. A very weak  
271 overturning cell appears in the Nordic Seas, promoting modest intermediate water formation  
272 (up to ~ 700 m, Fig. 6). The rates of global overturning in DO are thus greatly reduced  
273 relative to DC, increasing the residence time of water in the deep ocean.

274           The transition from a well-ventilated DC to a more stagnant DO ocean thereby drives  
275 accumulation of nutrients at depth and depletion in the intermediate and upper ocean in DO  
276 relative to DC because the reduced ventilation acts to ‘de-homogenize’ the ocean (Fig. 3c). In  
277 DC, the much stronger abyssal low latitudes upwelling allow nutrients to be more rapidly  
278 exported in the vigorous southward branch of the overturning circulation whereas in DO,  
279 these nutrient-rich waters are confined below 2000 m, thus increasing the nutrient  
280 concentrations below 2000 m and decreasing them above 2000 m in DO relative to DC.

281           In both simulations, nutrient-enriched waters are then carried to the surface by the  
282 Southern Ocean upwelling cells (Figs. 3a and 3b) but because of the intensity and shape of the  
283 overturning circulation, the upwelled waters contain more nutrients in DC relative to DO.  
284 This is why the subsurface nutrient concentrations between 40°S and 60°S decrease in DO.  
285 However, because the upwelling cells are deeper and expand slightly southward in DO, the  
286 subsurface of the highest latitude oceans (> 60°S) is enriched in nutrients relative to DC (Figs.  
287 3c and 4, again except for the upper 100 m in the Atlantic sector).

288           The decrease in subsurface nutrient concentration in the 40°S-60°S area in DO has  
289 important consequences for the low latitude nutrient supply. Indeed, the intermediate and  
290 modal waters (IMW) formed in this area are then advected to feed low latitude subsurface  
291 waters [Toggweiler and Samuels, 1993; Sarmiento *et al.*, 2004]. Because the IMW are poorer  
292 in nutrients when DP is open, the supply of nutrients to the low latitudes decreases. In  
293 addition, the slight increase in the tilt of the isopycnals in DO between 40°S and 50°S  
294 indicates that IMW sink deeper than in DC and consequently may contribute to the decrease  
295 in nutrient supply to the subsurface low latitudes waters in DO.

296           While low latitude productivity and export changes are well explained by the  
297 decreased nutrient availability resulting from the less dynamic DO ocean, additional processes  
298 contribute to the modelled changes in productivity in the Southern Ocean. Indeed, convective

299 mixing, associated with deep-water formation in winter and wind-driven circumpolar  
300 currents, heavily influences export productivity patterns at these latitudes (Figs. 1 and 6). In  
301 the Pacific sector, the DO deep-water convective areas are significantly shallower and  
302 narrower but remain deep enough to increase the productivity because the convection affects  
303 water masses significantly enhanced in nutrients. Following the onset of the ACC, a large  
304 convection zone appears in the southern Indian Ocean around 50°S, which, albeit relatively  
305 shallow (up to 500 m), drives a large increase in productivity (Fig. 1). Similarly, the wider  
306 convection zone just offshore Antarctica at the longitude of Africa generates productivity  
307 increase. Finally, in the Atlantic sector, the opposite occurs. Deep-water convection is  
308 completely shut down in DO in the central South Atlantic Ocean, leading to a substantial area  
309 of decreased productivity.

310         Because the PISCES model allows the explicit representation of nanophytoplankton  
311 and diatoms, we can also assess the role of these different groups in driving the modelled  
312 primary productivity changes (Fig. 7 and Supplementary Fig. 4). In the low latitudes, the  
313 decrease in primary productivity is essentially driven by a strong decline in  
314 nanophytoplankton productivity whereas diatom productivity, even if contributing much less  
315 to the total, remains relatively stable (except in the coastal Indian ocean). In contrast, in the  
316 mid- and high-latitudes, diatoms are responsible for a large part of primary productivity  
317 changes, and even become the main contributor to productivity changes in the highest  
318 latitudes (> 60°S). This is consistent with increased nutrient availability in the highest  
319 latitudes of the DO simulation due to the onset of the ACC. For instance, in the South Pacific,  
320 even if winter convection zones are shallower and narrower, the enhanced nutrient supply  
321 favours diatoms over nanophytoplankton.

322

323 **Discussion**

324 1. Comparison to model simulations

325 Numerous studies have investigated the role of DP on global climate, with varying  
326 continental configurations [e.g., *Mikolajewicz et al.*, 1993; *Heinze and Crowley*, 1997;  
327 *Toggweiler and Bjornsson*, 2000; *Sijp and England*, 2004; 2005; *Zhang et al.*, 2010; *Sijp et*  
328 *al.*, 2011; *Yang et al.*, 2014; *England et al.*, 2017]. Of these, the most relevant simulations to  
329 our study are those performed with the same continental configuration, in particular with the  
330 Panama seaway open [e.g., *Mikolajewicz et al.*, 1993; *Yang et al.*, 2014; *Fyke et al.*, 2015].  
331 Our reasoning here is based on the results of *Yang et al.* [2014] who demonstrated that the  
332 impacts of DP are strongly dependant upon the configuration of the Panama seaway. Using  
333 the CM2Mc model in a modern configuration (thus a closed Panama seaway), they show that  
334 the closure of DP leads to an ocean circulation resembling that of modern, with the notable  
335 exception of the suppression of the Antarctic Bottom Water cell in the Atlantic Ocean. This  
336 result is broadly confirmed by *England et al.* [2017], in which the same experiment with the  
337 fully coupled CSIRO Mk3L model demonstrates that the DP closed configuration exhibits  
338 similar rates of NADW and AABW relative to modern. On the contrary, with an open  
339 Panama seaway in an otherwise modern continental configuration, *Yang et al.* [2014] show  
340 that the closure of DP generates a large and wide Southern overturning cell and suppresses  
341 northern sinking. Our results, obtained with an open Panama seaway, are in agreement with  
342 the findings of *Yang et al.* [2014], but also with those of *Fyke et al.* [2015] and *Mikolajewicz*  
343 *et al.* [1993] who find a similar ocean circulation with a closed Drake – open Panama  
344 configuration, albeit with simpler models (EMIC or ocean-only models).

345 Ocean circulation in the presence of an open DP and an open Panama seaway (i.e., the  
346 impact of the opening of Panama) has also received considerable attention [e.g., *Mikolajewicz*  
347 *et al.*, 1993; *Lunt et al.*, 2008; *Sepulchre et al.*, 2014; *Yang et al.*, 2014; *Fyke et al.*, 2015]. All  
348 models ventilate the deep ocean from the South, although with reduced intensity than with a



349 closed DP, whereas the rates of deep-water formation in the North vary greatly between  
350 studies. *Yang et al.* [2014] find virtually no difference between a DO configuration with or  
351 without an open Panama seaway, that is, in both cases a strong NH deep overturning cell. In  
352 their simulations with the UVic model, *Fyke et al.* [2015] obtain a significant reduction in  
353 rates of NH deep water formation with an open Panama Gateway, albeit not a shutdown. A  
354 similar result is obtained by *Sepulchre et al.* [2014] with the IPSL-CM4 model and by *Lunt et*  
355 *al.* [2008] with the HadCM3 model. On the contrary, *Mikolajewicz et al.* [1993] find, with the  
356 ocean-only Hamburg model, that a Drake open and Panama open configuration leads to the  
357 cessation of the formation of NADW. In our runs, the thermohaline circulation induced by the  
358 DO configuration shows a weak NH intermediate water formation, which is close to the no-  
359 NADW state of *Mikolajewicz et al.* [1993]. It is interesting to note that the existence and  
360 vigour of the NADW rates in these different models might, at least in part, be driven by the  
361 geometry and size of the Panama gateway. Indeed, when Panama is closed (i.e. the modern  
362 state), all models show NADW formation. Models run with an open but narrow Panama  
363 seaway show reduced rates of NADW formation [*Lunt et al.*, 2008; *Sepulchre et al.*, 2014;  
364 *Fyke et al.*, 2015] and those run with a wide Panama seaway show NADW shutdown  
365 [*Mikolajewicz et al.*, 1993; this study]. Support for this finding comes from the simulations of  
366 *Sijp et al.* [2009] and *Sijp et al.* [2011]. In the first of these studies, open and closed DP  
367 simulations are performed in a modern continental configuration, that is, with a closed  
368 Panama seaway. Their DP open simulations yield significant NADW formation. In the second  
369 of these studies, coupled opening of DP and the Tasman gateway is simulated with the  
370 Eocene configuration of *Huber et al.* [2003], which features a wide Panama seaway.  
371 Interestingly, no NADW forms in these simulations. The simulations of *Yang et al.* [2014]  
372 yield contrasting results, however, because, with DP open, vigorous NADW rates exist  
373 regardless of whether a wide or a closed Panama seaway is prescribed. We tentatively infer

374 that the different boundary conditions (pCO<sub>2</sub> and ice sheets cover for instance) applied by  
375 *Yang et al.* [2014] and in our study may play a role. In particular, the effect of pCO<sub>2</sub> on ocean  
376 circulation may explain part of the discrepancy between the strong NADW rates found in the  
377 fully coupled GCM used by *Yang et al.* [2014] and our weak intermediate water formation  
378 state (see discussions in *Lunt et al.* [2010], *Donnadieu et al.* [2016] and *Winguth et al.*  
379 [2012]). In this regard, it is also interesting to note that the no-NADW simulations of *Sijp et*  
380 *al.* [2011] are run, as in our study, with elevated pCO<sub>2</sub>. Another factor that should not be  
381 ignored is that our fully coupled 1000 year GCM simulations can only be considered to have  
382 reached quasi-equilibrium and may miss further reorganizations of ocean circulation.  
383 However, although the Northern Hemisphere thermohaline state of the ocean differs between  
384 studies, we note that the dynamical results produced by our simulations are consistent with  
385 previous findings in that the opening of DP isolates Antarctica from warm and salty  
386 subtropical waters, which acts to freshen and cool most of the surface Southern Ocean  
387 (Supplementary Fig. 5). We conclude this climatic comparison by acknowledging that many  
388 important studies involving the opening of DP (or Tasman gateway) have been carried out  
389 using Eocene boundary conditions [e.g., *Huber et al.*, 2003; *Huber et al.*, 2004; *Huber and*  
390 *Nof*, 2006; *Zhang et al.*, 2010; *Sijp et al.*, 2011] but the idealized character of our modelling  
391 setup makes a direct comparison with these studies more questionable.

392 Two previous numerical studies are particularly relevant to our findings because they  
393 numerically address the impact of gateways opening on the biogeochemical state of the ocean,  
394 using the spatially resolved, albeit simpler, UVic climate-biogeochemical model [*Pagani et*  
395 *al.*, 2011; *Fyke et al.*, 2015]. In line with the findings of *Fyke et al.* [2015] (their figure 9),  
396 opening DP in our simulations increases DIC concentrations at depth in all basins although  
397 we do not observe a shift from a higher Atlantic DIC concentration to a higher Pacific DIC  
398 concentration (not shown). Our results also broadly agree with those of *Pagani et al.* [2011]

399 who show that the surface phosphate concentration in their Eocene simulation features a  
400 spatially uniform increase in the low latitudes and decrease in the southern high latitudes  
401 relative to modern, attributed to the shallower Eocene Southern Ocean upwelling cells relative  
402 to modern induced by the gateways configurations. However, in our experiments, the changes  
403 in surface nutrient concentrations in the southern high-latitudes are heterogeneous with areas  
404 of increase and decrease. Because we can unambiguously attribute the reorganization of  
405 surface nutrient concentration to DP opening in our simulations, we speculate that the  
406 gateways impact in the work of *Pagani et al.* [2011] is intertwined with other drivers, such as  
407 the much higher CO<sub>2</sub> concentration and other geographical characteristics imposed in their  
408 Eocene run relative to their modern.

409

## 410 2. Comparison to observations

411 Many data studies have investigated paleoproductivity changes during the Eocene and  
412 Oligocene [e.g., *Siesser*, 1995; *Diester-Haass and Zahn*, 1996; *Salamy and Zachos*, 1999;  
413 *Diester-Haass and Zahn*, 2001; *Diester-Haass and Zachos*, 2003; *Nilsen et al.*, 2003;  
414 *Schumacher and Lazarus*, 2004; *Dunkley Jones et al.*, 2008; *Griffith et al.*, 2010; *Coxall and*  
415 *Wilson*, 2011; *Egan et al.*, 2013; *Moore et al.*, 2014; *Plancq et al.*, 2014; *Villa et al.*, 2014]  
416 but the imprint of tectonics, particularly DP opening, is complex to decipher unambiguously  
417 because other climatic shifts, such as the EOT glaciation, occur contemporaneously.  
418 However, by investigating exclusively the effects of DP opening in a warmer world, our  
419 simulations provide insights on this possible imprint. It is particularly interesting to note that,  
420 when compared to records that span an interval longer than the EOT glaciation event, model  
421 results are qualitatively consistent with data (Fig. 1), suggesting that, if the DP was  
422 sufficiently well breached by the early Oligocene, at least part of the long-term  
423 paleoproductivity signal recorded in the data may be attributed to its opening. Our results

424 suggest that DP opening drove a significant reduction in paleoproductivity in the low latitude  
425 oceans – a finding consistent with long-term recorded changes, especially in the Eastern  
426 Equatorial Pacific [*Schumacher and Lazarus, 2004; Moore et al., 2014*] and in the Equatorial  
427 Indian Ocean [*Siesser, 1995*]. In the high latitudes, most long-term records document an  
428 increase in paleoproductivity [e.g., *Diester-Haass and Zahn, 1996; 2001; Schumacher and*  
429 *Lazarus, 2004*], but the pattern of paleoproductivity increase/decrease simulated by the model  
430 is not uniform and strongly related to variations in the convective mixing areas.

431 Our simple model-data comparison is similar to that of *Winguth et al. [2012]*. A more  
432 in-depth analysis is unwarranted because we present a paleogeography sensitivity simulation  
433 rather than an attempt to simulate Eocene-Oligocene events *sensu stricto*. Furthermore,  
434 different data sets produce sometimes contrasting indications of paleoproductivity change  
435 even when taken from the same site. A good example comes in the paleoproductivity records  
436 from the Eastern Equatorial Pacific [e.g., *Coxall and Wilson, 2011; Erhardt et al., 2013;*  
437 *Moore et al., 2014*]. Although there are reasonable explanations to these discrepancies  
438 [*Erhardt et al., 2013; Moore et al., 2014*], this observation highlights the complexity  
439 associated with reconstructing paleoproductivity from proxy signals [*Anderson and Delaney,*  
440 *2005*]. In the high latitudes, many records show significant enhancement of the  
441 paleoproductivity during the EOT event [e.g., *Salamy and Zachos, 1999; Diester-Haass and*  
442 *Zahn, 2001; Planq et al., 2014; Villa et al., 2014*] or during the latest Eocene [*Diekmann et*  
443 *al., 2004; Egan et al., 2013; Villa et al., 2014*]. In particular, during the latter, it has been  
444 argued that pulses of tectonic opening of DP [*Scher and Martin, 2006*] may play a role in the  
445 transition from oligotrophic to eutrophic nannofossils taxa [*Villa et al., 2014*] or an increase  
446 in diatom abundance [*Egan et al., 2013*]. Based on Si isotopes records, *Egan et al. [2013]*  
447 invoke increased diatom primary productivity to explain the recorded increased silicic acid  
448 utilization at the surface at Site 1090. Although our modelled results support a net decrease in

449 diatoms (and nanophytoplankton) primary production in most of the South Atlantic Ocean  
450 (Fig. 7), the simulated export production increases at Sites 689 [Villa *et al.*, 2014] and 1090  
451 [Egan *et al.*, 2013]. Primary and export productivity do indeed not necessarily co-vary as  
452 organic matter remineralization, among others, is a function of temperature [John *et al.*,  
453 2013]. The significant modelled surface cooling when DP opens at Sites 689 and 1090  
454 (Supplementary Fig. 5) generates reduced recycling of organic matter and may thus explain  
455 the contrasting variations of primary and export productivity.

456

### 457 3. Caveats related to the idealized framework of the study

458       Taken at face value, our simulated paleoproductivity changes fit marine records  
459 reasonably well, but important caveats must be kept in mind when interpreting our model  
460 results. First, we do not use a realistic late Eocene global paleogeography, either regarding the  
461 geometry of important gateways or other major tectonic differences such as the existence of  
462 the Tethys Sea or the position and height of the Tibetan Plateau. Our idealized simulations  
463 therefore remain a sensitivity experiment to the opening of DP. Because our simulated  
464 paleoproductivity changes are essentially driven by the onset of the ACC, the impact of a  
465 closed or restricted Tasman seaway prior to the latest Eocene [Huber *et al.*, 2004; Stickley *et*  
466 *al.*, 2004] may have important consequences for paleoproductivity patterns. However, a  
467 recent idealized study suggests that a circumpolar water path, which would circumvent  
468 Australia, could exist even in the absence of an open Tasman seaway [Munday *et al.*, 2015].  
469 Second, our simulations were performed using two end-member boundary conditions (DP  
470 closed and DP open) that are not strictly representative of the late Eocene and Oligocene, as  
471 some evidence points to initial opening of DP as early as the Early Eocene [Eagles *et al.*,  
472 2006; Eagles and Jokat, 2014]. The climatic relevance of an incipient opening is intuitively  
473 questionable and the concept of a threshold relationship between gateway opening and

474 climate response is appealing. *Sijp and England* [2005] argued that the sill depth of DP  
475 critically impacted the global ocean circulation, because it was instrumental in controlling the  
476 formation of NADW, but this result was obtained with a closed Panama Seaway, which is a  
477 configuration that favours NADW formation [*Lunt et al.*, 2008; *Sepulchre et al.*, 2014; *Yang*  
478 *et al.*, 2014]. The open Panama simulations performed here are not sufficient to  
479 unambiguously answer this question. Finally, our offline PISCES simulations are run with  
480 fixed nutrient supply from rivers, which are unaffected by variations in runoff whereas we  
481 know that changes in nutrient and carbonate supply down rivers across the Eocene Oligocene  
482 Transition are both likely and capable of driving major change in global carbon cycling  
483 [*Coxall et al.*, 2005; *Dunkley Jones et al.*, 2008; *Merico et al.*, 2008; *Armstrong McKay et al.*,  
484 2016].

485

## 486 **Conclusion**

487 Using the IPSL-CM5A coupled model we have shown that the opening of Drake  
488 Passage profoundly alters oceanic paleoproductivity patterns across the globe. The  
489 reorganization of the oceanic circulation, from a well-ventilated ocean when Drake Passage is  
490 closed to a more stagnant state when Drake Passage is open, drives subsurface nutrient  
491 depletion in the low latitudes. Nanophytoplankton, rather than diatoms – possibly because the  
492 latter are only marginal contributors to the modelled low latitude primary productivity, are  
493 strongly affected by this depletion and the productivity consequently declines, especially in  
494 the Pacific and Indian oceans. In the high latitudes, productivity changes are driven both by  
495 nutrient availability and areas of convective mixing, which generate zones of productivity  
496 increase (most of the southern Pacific and Indian oceans) and decrease (most of the South  
497 Atlantic Ocean). In contrast to the low latitudes, diatoms are largely responsible for these  
498 productivity variations, especially in the southernmost latitudes. A simple qualitative

499 comparison with geological records reveals a good match between locations of  
500 paleoproductivity changes simulated by the model and inferred from data, suggesting that the  
501 role of Drake Passage opening in driving part of the long-term productivity signal across the  
502 late Eocene and early Oligocene may be non-negligible.

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534

535 **Author Contributions**

536 J.-B.L. designed and performed the numerical simulations, with contributions from Y.D., and  
537 wrote the draft of the manuscript. All authors analysed and discussed the results and  
538 contributed to the final version of the manuscript.

539

540 **Additional Information**

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## 794 **Legends and Tables**

795

Site (Reference)	Latitude	Longitude	Qualitative productivity change
1209-1211 (Griffith et al. 2010)	~ 20°N	~ 172°W	decrease
925 (Nilsen et al. 2003) *	~ 4°N	~ 43°W	no change
U1333 (Moore et al. 2014)	~ 3°N	~ 113°W	decrease
1218 and U1334 (Moore et al. 2014)	~ 0-2°N	~ 110°W	decrease
462 (Schumacher and Lazarus 2004)	~ 2°S	~ 178°W	no change
959 (Schumacher and Lazarus 2004)	~ 2°S	~ 13°W	slight decrease or no change
574 (Schumacher and Lazarus 2004)	~ 7°S	~ 117°W	slight decrease or no change
709 (Siesser 1995)	~ 10°S	~ 75°E	decrease
758 (Siesser 1995)	~ 10°S	~ 110°E	no change or no data
757 (Siesser 1995)	~ 30°S	~ 95°E	no change
762 (Siesser 1995)	~ 35°S	~ 115°E	decrease
763 (Diester-Haas and Zahn 2001)	~ 40°S	~ 112°E	increase
1090 (Diekmann et al. 2004)	~ 43°S	~ 9°E	decrease
1090 (Egan et al. 2013)	~ 43°S	~ 9°E	increase
752 (Siesser 1995)	~ 45°S	~ 90°E	no change or no data
511 (Plancq et al. 2014)	~ 52°S	~ 42°W	increase
511 (Schumacher and Lazarus 2004)	~ 55°S	~ 42°W	increase
748 (Siesser 1995)	~ 55°S	~ 70°E	no change or no data
592 (Diester-Haas and Zahn 2001)	~ 55°S	~ 165°E	increase
748 (Schumacher and Lazarus 2004)	~ 56°S	~ 73°E	increase
748 (Villa et al. 2014)	~ 57°S	~ 74°E	increase
738 and 744 (Villa et al. 2014) *	~ 63°S	~ 83°E	increase
689 (Schumacher and Lazarus 2004)	~ 72°S	~ 15°W	increase
689 and 690 (Villa et al. 2014)	~ 72°S	~ 15°W	increase

**Table 1.** Compilation of long-term productivity changes across the late Eocene and early Oligocene. Longitudes and latitudes are approximate paleolocations of the sites. The asterisk denotes sites where modern location is used. There are a few redundant sites but findings from different studies at these sites are similar.

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798 **Figure 1.** (top) Mean annual export production at 100 m ( $\text{gC.m}^{-2}.\text{yr}^{-1}$ ) for DC and DO  
799 simulations. (bottom) Annual export production at 100 m difference between DO and DC  
800 ( $\text{gC.m}^{-2}.\text{yr}^{-1}$ ). Color-coded circles represent productivity variations from data records (see  
801 Table 1): red = increase, blue = decrease, pale shading = weak or uncertain variations, white =  
802 no variations or lack of data.  
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805 **Figure 2.** Zonally averaged export production at 100 m ( $\text{gC.m}^{-2}.\text{yr}^{-1}$ ) at the global scale and in  
806 each basin for DC (black solid lines) and DO (red dashed lines).  
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809 **Figure 3.** (top) Mean annual zonally averaged nitrate concentration ( $\mu\text{mol.L}^{-1}$ ) for DC and  
810 DO with density contours ( $0.1 \text{ kg.m}^{-3}$ ) overlain. (bottom) Mean annual zonally averaged  
811 nitrate concentration difference ( $\mu\text{mol.L}^{-1}$ ) between DO and DC, with density contours ( $0.1$   
812  $\text{kg.m}^{-3}$ ) overlain in black for DC and green for DO. Note that  $1000 \text{ kg.m}^{-3}$  is subtracted from  
813 density values on the plot.  
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816 **Figure 4.** Global, Atlantic, Pacific and Indian upper 500 m nitrate concentration gradients in  
817 the low latitudes ( $40^{\circ}\text{S} - 40^{\circ}\text{N}$ , solid lines) and the southern high latitudes ( $90^{\circ}\text{S} - 60^{\circ}\text{S}$ ,  
818 dashed lines) for DC (black) and DO (red).  
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821 **Figure 5.** Global meridional overturning streamfunction ( $\text{Sv}$ , clockwise positive) for DC and  
822 DO. Contours 4  $\text{Sv}$ , negative dashed.  
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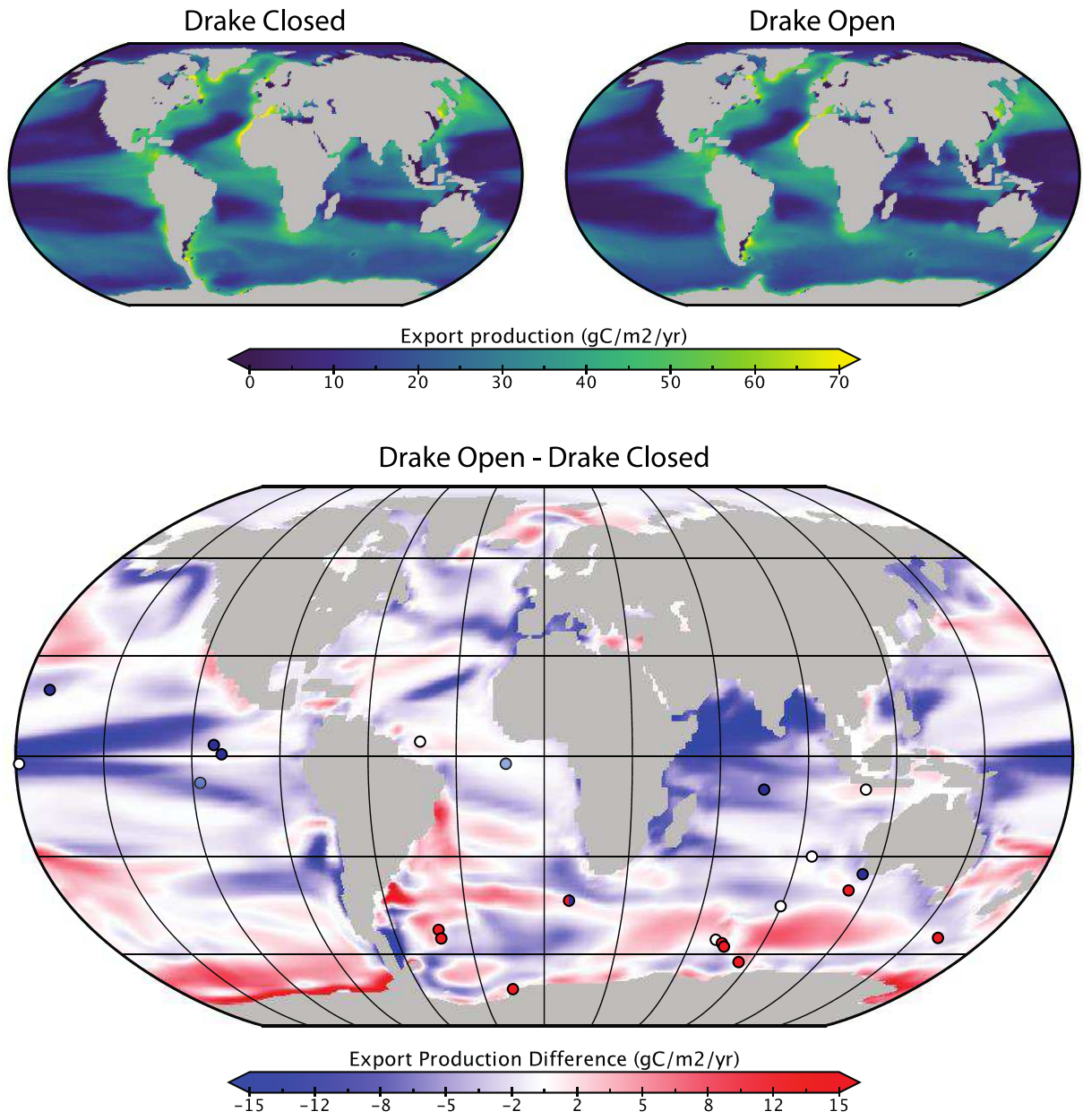
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825 **Figure 6.** Wintertime deep-water formation in the Southern (top) and Northern (bottom)  
826 Hemispheres for DF and DO simulations, as represented by the ocean mixed-layer depth (m).  
827 Note that the scale differs between southern and northern plots.  
828

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830 **Figure 7.** Diatoms and nanophytoplankton primary production difference ( $\text{gC.m}^{-2}.\text{yr}^{-1}$ )  
831 between DO and DC.  
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**Figure 1.**

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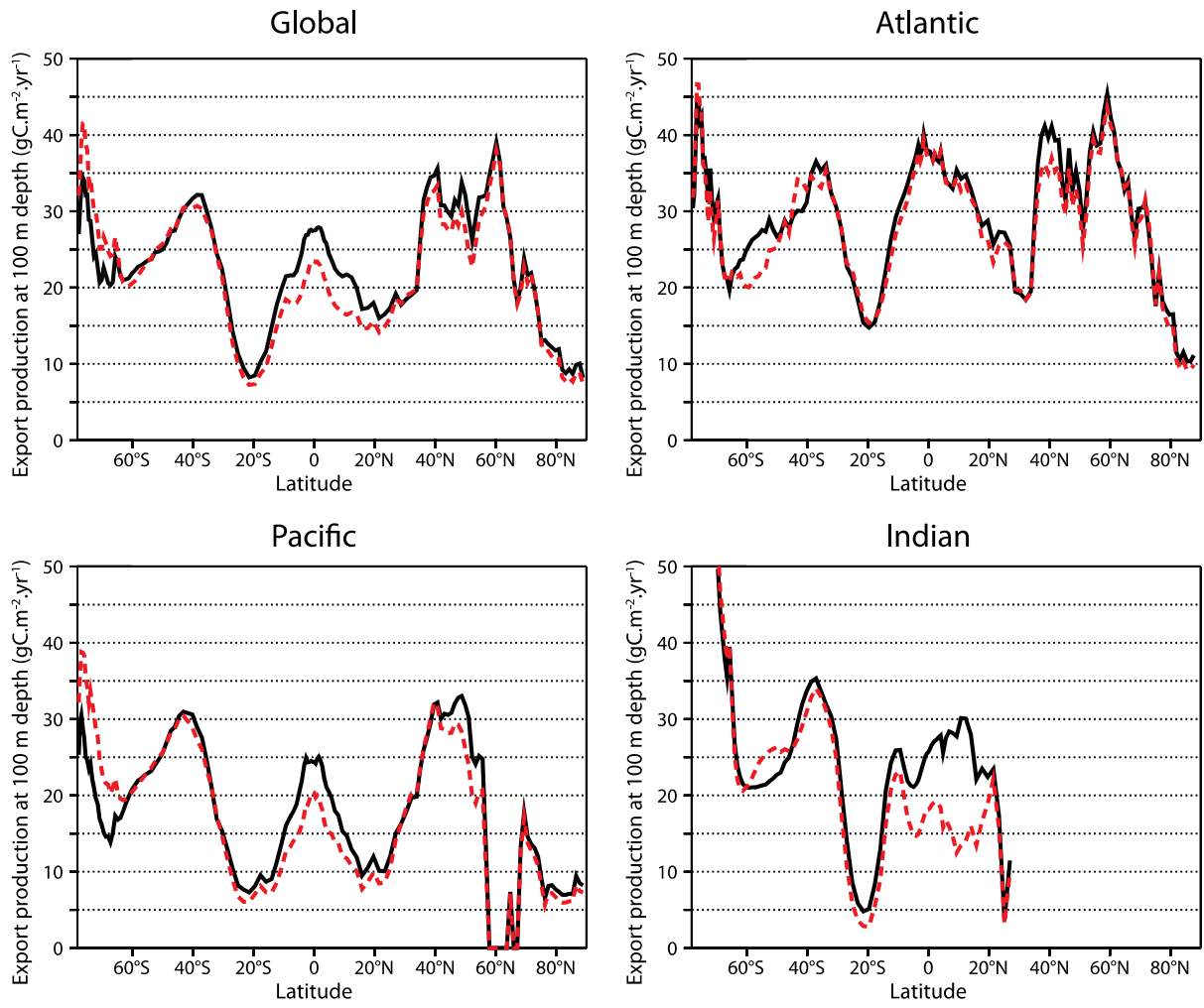
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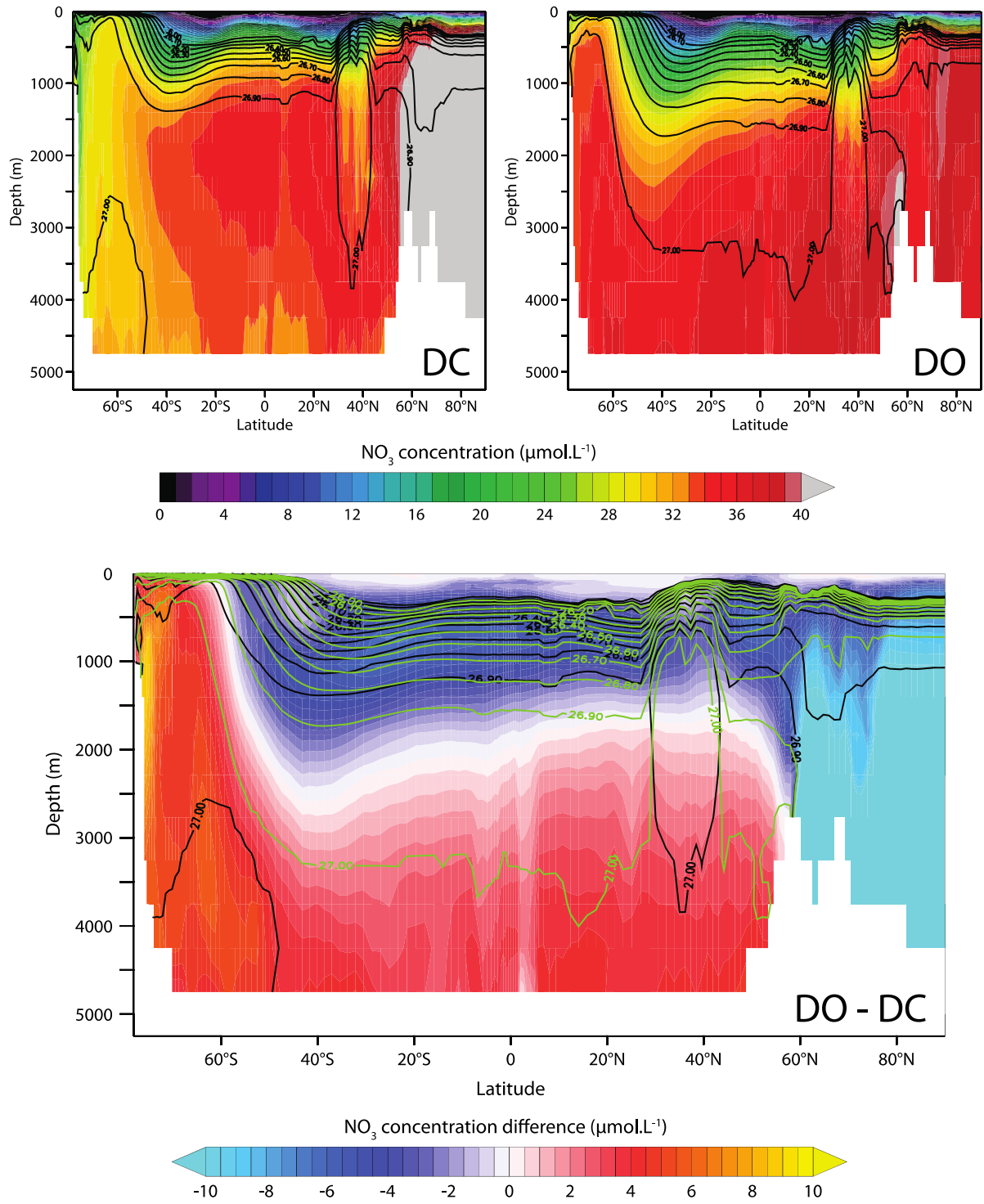
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**Figure 2.**



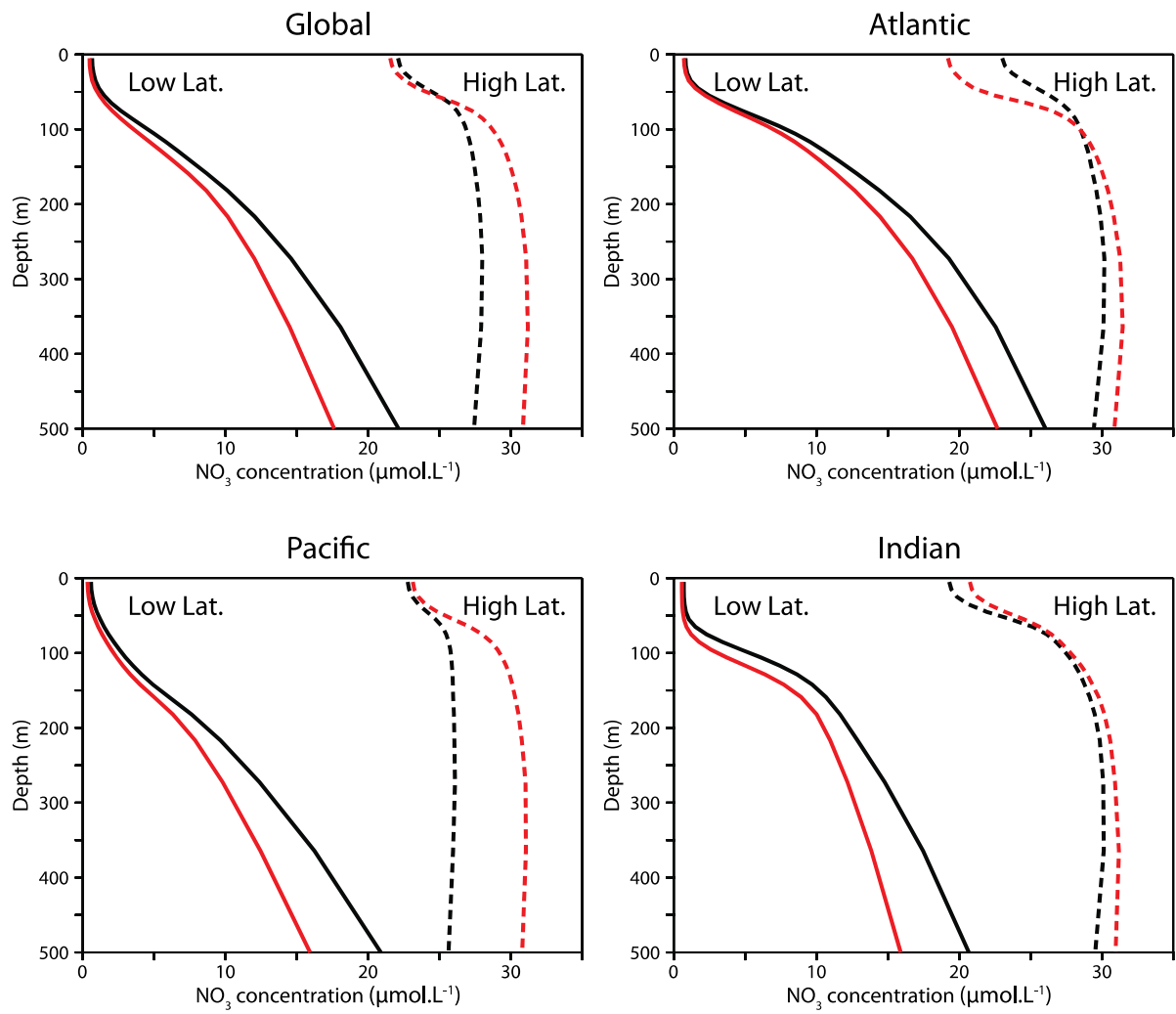
**Figure 3.**

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**Figure 4.**

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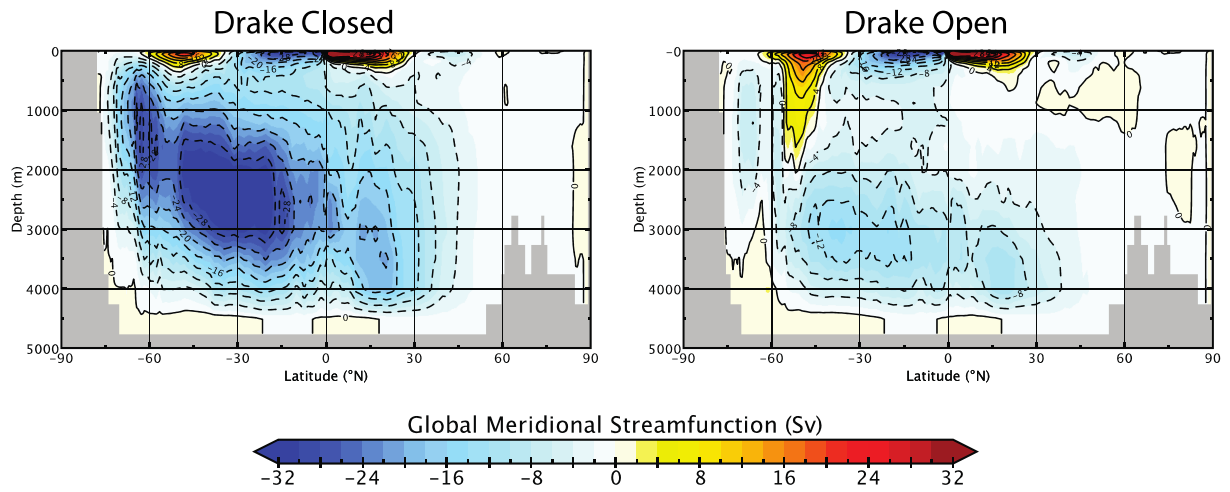
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**Figure 5.**

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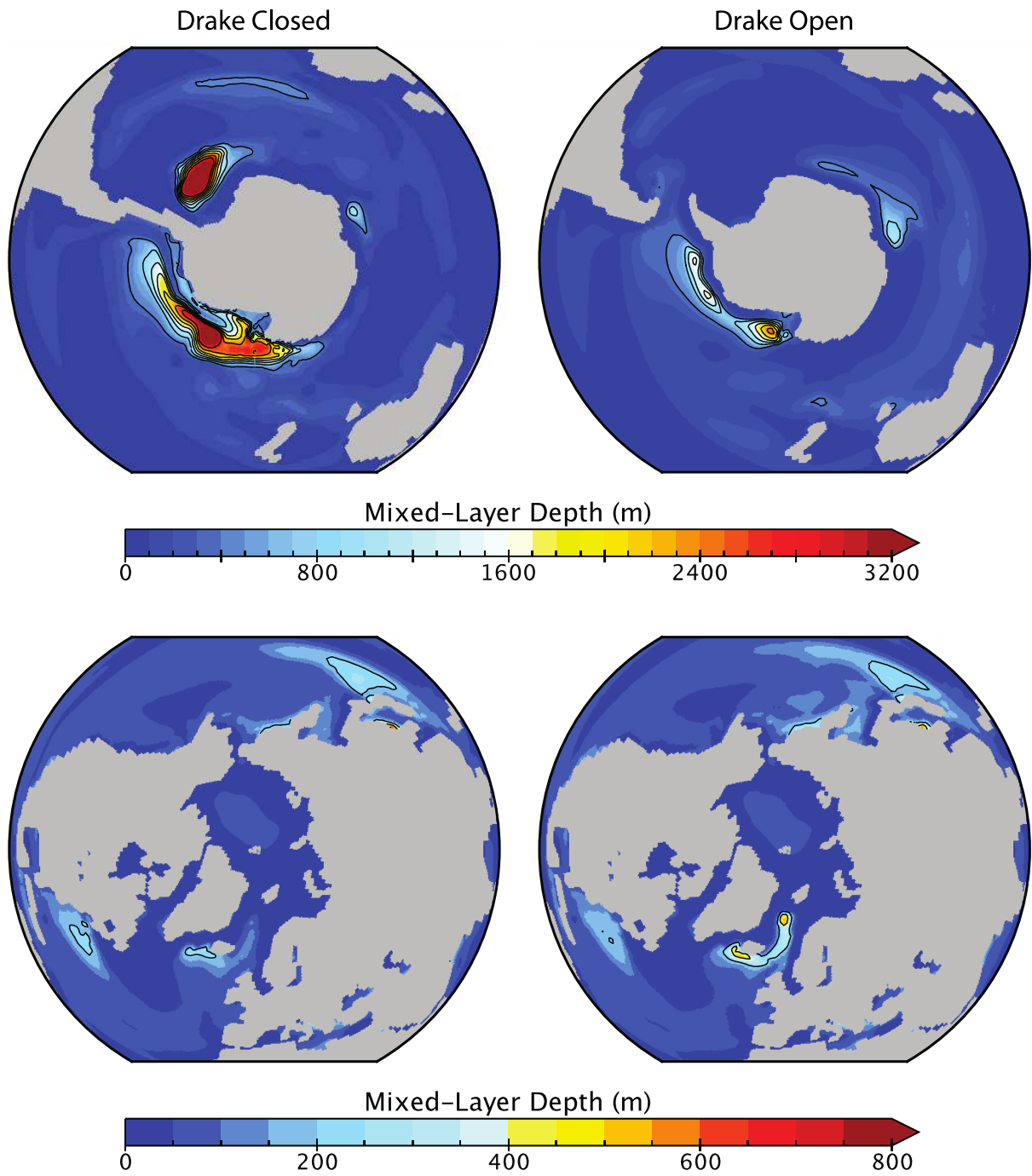
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**Figure 6.**

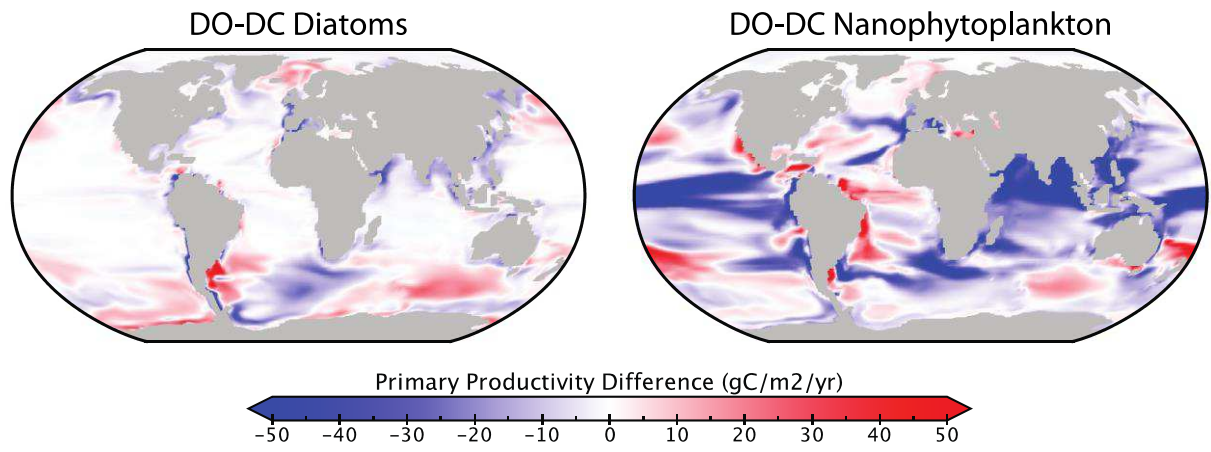
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**Figure 7.**

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