



## 1 How does the phytoplankton-light feedback affect marine N<sub>2</sub>O inventory?

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10

### 11 Abstract

12

13 The phytoplankton-light feedback (PLF) depicts how phytoplankton biomass interacts with the  
14 downwelling shortwave radiation entering the ocean. Considering the PLF allows differential  
15 heating across the ocean water column as a function of the phytoplankton concentration. Only  
16 one third of the CMIP6 Earth system models include a complete representation of the PLF. In  
17 other models, the PLF is mimicked either thanks to a prescribed climatology of chlorophyll or  
18 not represented at all. Consequences of an incomplete representation of the PLF on the marine  
19 biogeochemical content haven't been assessed yet and remain a source of multi-model  
20 uncertainty in future projection. Here, we scrutinize with a single modelling set-up how various  
21 representation of the PLF can impact ocean physics and ultimately marine production of a  
22 major greenhouse gas, the nitrous oxide (N<sub>2</sub>O). Global sensitivity experiments considering the  
23 ocean, sea ice and marine biogeochemistry have been performed at 1-degree of horizontal  
24 resolution over the last two decades (1999-2018). We show that the representation of the PLF  
25 has significant consequences on the ocean heat uptake and temperature of the first 300 meters  
26 of the tropical ocean. Temperature anomalies due to an incomplete PLF representation drive  
27 perturbations of the ocean stratification, dynamics and oxygen concentration. Different  
28 projection pathways for N<sub>2</sub>O production result from the choice of the PLF representation.  
29 Considering an incomplete representation of the PLF overestimates the oxygen concentration  
30 in the North-Pacific oxygen minimum zone and underestimates the local N<sub>2</sub>O production. This  
31 leads to important regional differences of sea-to-air N<sub>2</sub>O fluxes: fluxes are enhanced by up to  
32 24% in the south Pacific and south Atlantic subtropical gyres, but reduced by up to 12% in  
33 oxygen minimum zones of the northern hemisphere. Our results based on a global ocean-  
34 biogeochemical model at CMIP6 state-of-the-art thus shine a light on a current uncertainty of  
35 the modelled marine nitrous oxide budget in that climate models.

36

### 37 Plain language summary

38

39 Phytoplankton absorbs the solar radiation entering the ocean surface, and contributes to keep  
40 the associated energy in surface waters. This natural effect is not commonly represented in the  
41 oceanic part of climate models, or often suffers simplifications. We show that an incomplete  
42 representation of this biophysical interaction affects the way climate models capture ocean  
43 warming, what in turn uncertain the forecast of oceanic emissions of an important greenhouse  
44 gas called the nitrous oxide.

45

46 **Key-words:** phytoplankton-light interaction; bio-physical feedback; nitrous oxide; N<sub>2</sub>O; CMIP6  
47 Earth system models; CNRM-ESM2-1; ocean-biogeochemical model; greenhouse gases; marine  
48 emission; climate



49

50 **Key points:**

- 51 - forced ocean-biogeochemical experiments reveal that marine production of nitrous oxide is
- 52 sensitive to the representation of the phytoplankton-light feedback
- 53 - the phytoplankton-light feedback perturbs the accumulation of heat and the ocean
- 54 dynamics which drive changes in nitrous oxide production patterns
- 55 - an incomplete phytoplankton-light feedback overestimates sea-to-air N<sub>2</sub>O fluxes by up to
- 56 24% in subtropical gyres and reduces them by up to 12% in oxygen minimum zones

57

58 **1. Introduction**

59

60 Couplings between the physical, biogeochemical, or ecosystem compartments of the ocean  
61 can induce abrupt system changes (Heinze et al., 2021). Currently, the only coupling in Earth  
62 system models existing between modelled marine biogeochemistry and ocean dynamics is the  
63 interactive phytoplankton-light feedback (PLF) (Séférian et al., 2020). It is at play when the  
64 chlorophyll (CHL) produced by the biogeochemical compartment is used to determine the  
65 fraction of shortwave radiation (SW) penetrating into the ocean surface waters. In this case,  
66 the CHL concentration mimicking the influence of the marine biota on the vertical  
67 redistribution of heat in the upper ocean is consistent (because the same) with the one used  
68 to compute biogeochemical cyclings.

69

70 **a) Phytoplankton-light feedback (PLF)**

71

72 Since the first observational evidences on how surface materials may impact light absorption  
73 by the ocean and change the radiative imbalance within the mixed-layer depth (Kahru et al.  
74 1993), several ocean models have gradually accounted for this biophysical interaction. Gildor  
75 and Naik (2005) highlighted the importance to consider monthly variations of CHL to capture  
76 the first-order effect of marine biota on light penetration in ocean models. Then, introducing a  
77 light-interactive CHL in numerical experiments has been shown to affect oceanic phenomena  
78 on a wide range of spatial and temporal scales. Enabling a phytoplankton-light interaction  
79 modifies the intensity of the spring-bloom in subpolar regions (Oschlies, 2004), the  
80 maintenance of the Pacific Cold Tongue (Anderson et al., 2007), the seasonality of the Arctic  
81 Ocean (Lengaigne et al., 2009), the strength of the tropical Pacific annual cycle and the ENSO  
82 variability (Timmermann and Jin, 2002; Marzeion et al., 2005), the northward extension of the  
83 meridional overturning circulation (Patara et al., 2012), and the cooling of the Atlantic and Peru-  
84 Chili upwelling systems (Hernandez et al., 2017, Echevin et al., 2022).

85

86 However the mean effect of the PLF on sea surface temperature (SST) has been argued to  
87 depend on the numerical framework (forced ocean versus coupled ocean-atmosphere models).  
88 The conflicting results obtained on that topic in the literature have been shown to be mainly  
89 due to diverging bio-optical protocols among models rather than by the inclusion of air-sea  
90 coupling. Following Park et al. (2014) the atmosphere-ocean coupling just acts to amplify the  
91 PLF-induced mean change, but does not alter the sign of the response obtained in ocean-only  
92 experiments. Two main causal chains have been proposed to interpret the sign of the final heat  
93 perturbation, opposing the proeminence of an indirect dynamical response (Murtugudde et al.,  
94 2002; Löptien et al., 2009) to that of a direct thermal effect (Mignot et al., 2013; Hernandez et  
95 al., 2017). Regional dependencies of these two mechanisms have also been evidenced (Park et



96 al., 2014). However, beyond the diversity of model responses, a consensus emerges about the  
97 first order effect the PLF exerts on the ocean, being to perturb the ocean thermal structure  
98 (Nakamoto et al., 2001; Murtugude et al., 2002; Oschlies, 2004; Manizza et al., 2005, 2008;  
99 Anderson et al., 2007; Lengaigne et al., 2007; Gnanadesikan and Anderson, 2009; Löptien et  
100 al., 2009; Patara et al., 2012; Mignot et al., 2013; Hernandez et al., 2017). By trapping more  
101 heat at the ocean surface in eutrophic regions, such as coastal or equatorial upwellings areas,  
102 the presence of phytoplankton increases the surface warming. Confining heat at the surface  
103 leads to less heat penetrating into the ocean interior. Because these effects depend on upper  
104 ocean stratification, they are more active during local summer and at low latitudes. An  
105 important role is attributed to modelled seasonal deepening of the mixed layer as it determines  
106 the intensity of the underlying temperature anomaly and its vertical movement to the surface.  
107 In other terms, whatever the temporality of the causal chain, changes in the PLF representation  
108 are expected to both perturb the ocean heat uptake, and trigger perturbations of both the water  
109 column stratification and associated ocean dynamics.

110  
111 **b) This study: implications for N<sub>2</sub>O budget uncertainties**  
112

113 Nitrous oxide (N<sub>2</sub>O) is a major ozone-depleting substance (Ravishankara et al., 2009; Freing et  
114 al., 2012) and a potent greenhouse gas, whose global warming potential is 265–298 times that  
115 of CO<sub>2</sub> for a 100-year timescale (Myhre et al., 2013). The spatial coincidence between marine  
116 productive areas and observed hot-spots of N<sub>2</sub>O production leads to question the impact of an  
117 incomplete representation of the PLF on the simulated N<sub>2</sub>O inventory. Indeed recent  
118 observational studies highlight that N<sub>2</sub>O production is high in low-oxygen tropical regions and  
119 cold upwelling waters (Arévalo-Martínez et al 2018; 2020; Yang et al., 2020; Wilson et al., 2020).  
120 N<sub>2</sub>O has been shown to become more highly saturated in the surface waters of equatorial  
121 upwelling regions due to the upward advection of N<sub>2</sub>O-rich waters (Arévalo-Martínez et al.,  
122 2017). Thus, regions known to account for the most productive areas of the ocean spatially  
123 coincide with the highest N<sub>2</sub>O production: 64% of the annual N<sub>2</sub>O flux occurs in the tropics,  
124 and 20% in coastal upwelling systems that occupy less than 3% of the ocean area (Yang et al.,  
125 2020).

126  
127 Despite these recent results, a large range of uncertainties still surrounds oceanic N<sub>2</sub>O  
128 emissions, as large areas of both the open and coastal ocean remain undersampled by  
129 observations (Wilson et al., 2020). In particular, the sparsity of observational data in regions  
130 which emit considerable amounts of this gas contributes to increase the uncertainties. The  
131 recent global budget of Tian et al. (2020) estimates natural sources from soils and oceans  
132 contributing up to 57% to the total N<sub>2</sub>O emissions for the recent decade, with the ocean flux  
133 reaching 3.4 (2.5–4.3) Tg N yr<sup>-1</sup>. But this oceanic contribution reflects a large uncertainty range,  
134 as it has been computed based on global ocean-biogeochemical models (and moreover based  
135 on a very small number of models). Indeed very few climate models, even in the current CMIP6  
136 generation, include emissions (and beforehand a complete representation of N cycling) of N<sub>2</sub>O  
137 fluxes: only 4 out of the 26 Earth system models considered in Sférian et al. (2020) model  
138 marine N<sub>2</sub>O emissions.

139  
140 Finally, this last generation of Earth system models projects an enhanced ocean warming in  
141 response to climate change, which is in turn expected to increase upper-ocean stratification  
142 (Sallée et al., 2021) and to contribute to greater reductions in upper-ocean nitrate and



143 subsurface oxygen ventilation (Kwiatkowski et al., 2020). Ocean warming and deoxygenation  
144 constitute two triggers of high-probability high-impact climate tipping points (Heinze et al.,  
145 2021), which have been identified as two of the main environmental factors influencing marine  
146 nitrous oxide (N<sub>2</sub>O) distributions (IPCC, 2019; Hutchins and Capone, 2022). Through the  
147 addition of its expected imprints on the upper ocean stratification, the PLF representation could  
148 further change the oceanic N<sub>2</sub>O source by modulating the mixing between N<sub>2</sub>O-rich water and  
149 intermediate depths, perturbing the way N<sub>2</sub>O-rich water reach the air-sea interface (Freing et  
150 al., 2012).

151  
152 In that perspective, the present study investigates how an incomplete representation of the  
153 phytoplankton-light feedback may particularly uncertain nitrous oxide prediction in an up-to-  
154 date global ocean-biogeochemical model making up the current generation of Earth system  
155 models. Section 2 describes the numerical model and the set of experiments encompassing the  
156 existing options to consider CHL modulations of the incoming SW radiation. The N<sub>2</sub>O  
157 parametrization used in this model is also detailed. Section 3 presents the important effect of  
158 an interactive PLF on the ocean heat content, associated ocean stratification and dynamics,  
159 and its repercussions on marine N<sub>2</sub>O inventory. Finally, Section 4 summarizes the main results,  
160 addresses their broader implications, and discusses the future work motivated by this study.

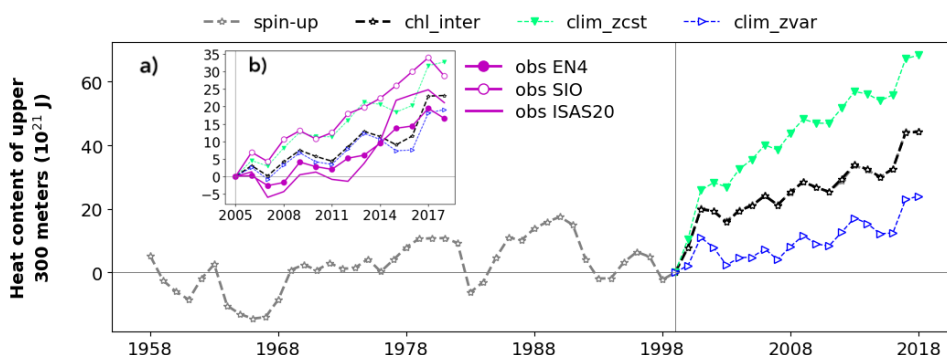
## 161 162 **2. Methodology**

### 163 164 **a) Sensitivity experiments with a global ocean-biogeochemical model**

165  
166 Recent projections of future N<sub>2</sub>O emissions realized as part of intercomparison projects like  
167 CMIP6 are still based on Earth system models with a low spatial resolution (Séférián et al.,  
168 2020). For sake of coherence with CMIP biogeochemical modelling efforts, we use a global  
169 ocean-biogeochemical configuration of the NEMO-PISCES model (Madec, 2008; Aumont et al.,  
170 2015) at 1° of horizontal resolution in the following. This model corresponds to the oceanic  
171 component of CNRM-ESM2-1 (Séférián et al., 2019) and is one of the few CMIP6-class models  
172 that contributed to the Global N<sub>2</sub>O budget (Tian et al., 2020). Details on model configuration  
173 are given in Berthet et al. (2019). Using an ocean-only configuration allows to isolate the local  
174 response induced by the PLF, by not confounding it with potential inter-basin feedbacks acting  
175 through the atmosphere.

176  
177 The global ORCA1 domain was first spun-up under preindustrial conditions during 2000 years  
178 by cycling the first 5 years of the JRA55-do atmospheric reanalysis (Tsujino et al., 2018; i.e.  
179 OMIP2 compliant: Tsujino et al., 2020). The cycling method was prolonged until year 1958,  
180 while considering the historical evolution of atmospheric CO<sub>2</sub> and N<sub>2</sub>O since year 1850. Then  
181 the complete period of JRA55-do atmospheric forcing has been rolled out from 1958 to 2018.  
182 This first experiment (hereafter chl\_inter) together with the spin-up both account for an  
183 interactive PLF: the penetration of SW radiation into the ocean surface is constrained by the  
184 CHL concentration produced by the PISCES biogeochemical component. Hereafter the term  
185 "spin-up" has been extended to the whole period simulated before year 1999.

186



187  
 188 Figure 1: Modelled **tropical [35°S-35°N] heat content of upper 300 m** (OHC300; in ZJ) for each  
 189 experiment described in Table 1: chl\_inter (black; empty stars), clim\_zcst (green; full downward  
 190 triangles) and clim\_zvar (blue; empty rightward triangles). In (a) final part of the spin-up has  
 191 been added in gray to illustrate the branching protocol in year 1999, and OHC300 anomalies  
 192 have been computed with respect to year 1999. Subplot (b) zooms over the Argo period to  
 193 compare modelled tropical OHC300 anomalies with 3 in situ-based products (see section 2c).  
 194

195 At year 1999 two other sensitivity experiments were branched off (Figure 1). The experiments  
 196 clim\_zcst and clim\_zvar account for an incomplete and external PLF, as they consider an  
 197 observed climatology of surface CHL from ESACCI (Valente et al., 2016) in order to compute the  
 198 light penetration into sea water. These two experiments differ from each other by the "realism"  
 199 of the vertical profile derived from the ESACCI CHL surface climatology (Table 1). The vertical  
 200 profile used for clim\_zcst is considered **constant** and spreads uniformly in the vertical direction  
 201 to the level below which we consider the light cannot penetrate (Figure S1, b and d-f). The CHL  
 202 vertical profile of clim\_zvar is **variable** and derived from the 2D surface climatology following  
 203 Morel and Berthon (1989) to the level of light extinction (Figure S1, c and d-f). This set of  
 204 experiments is representative of the several configurations used in the case of CMIP  
 205 intercomparison project.  
 206  
 207

Experiment	Which CHL fields to interact with incoming SW radiation?	PLF nature
chl_inter	uses directly the 3D CHL produced by the biogeochemical component	interactive
clim_zcst	uses the prescribed monthly climatology of ESACCI CHL with a constant vertical profile, equal to the value of the surface climatology up to the level of light extinction	incomplete
clim_zvar	uses the prescribed monthly climatology of ESACCI CHL with a variable vertical profile, derived from the surface climatology following Morel and Berthon (1989)	incomplete

208  
 209 Table 1: Experimental set-up.  
 210



211 Note that in `clim_zcst` and `clim_zvar`, CHL concentrations used for radiation and  
212 biogeochemical cycles are decoupled: the biogeochemical model produces CHL and uses it for  
213 biogeochemical element cycling but feedback of CHL on physics (stratification, ocean heat  
214 content) is determined by the externally prescribed CHL climatology. In this case the marine  
215 biota computed by the biogeochemical model does not affect the physical properties of the  
216 ocean waters.

217  
218 Finally, all three experiments use a simplified formulation of light absorption by the ocean to  
219 calculate both the phytoplankton light limitation in PISCES and the oceanic heating rate  
220 (Lengaigne et al., 2007). In this formulation, visible light is split into three wavebands: blue  
221 (400–500 nm), green (500–600 nm) and red (600–700 nm); for each waveband, the CHL-  
222 dependent attenuation coefficient is fitted to the coefficients computed from the full spectral  
223 model of Morel (1988) (as modified by Morel and Maritorena (2001)) assuming the same  
224 power-law expression.

225  
226 Consequences on the marine biogeochemical mean state of incomplete representations of the  
227 PLF are assessed in the following by difference with our control run `chl_inter`. This methodology  
228 allows to evaluate how different levels of realism and complexity in resolving bio-physical  
229 interactions impact the physical and biogeochemical content of the modelled ocean.

230

### 231 **b) N<sub>2</sub>O parameterization**

232

233 As described by Aumont et al. (2015), PISCES models five limiting nutrients for phytoplankton  
234 growth: nitrate and ammonium, phosphate, silicate and iron. The phosphate, nitrate-  
235 ammonium nutrient pools are not really independent in PISCES, as they are linked by a constant  
236 and identical Redfield ratio in all the modelled organic compartments. Redfield ratios are set to  
237 122:16:1 for C:N:P following Takahashi et al. (1985) and the -O:C ratio is set to 1.34 (Kortzinger  
238 et al., 2001).

239

240 In the ocean, N<sub>2</sub>O production and consumption are driven by marine bacteria in slightly  
241 oxygenated waters. N<sub>2</sub>O can occur as a by-product during microbial nitrification and as an  
242 intermediate product during denitrification (Freing et al., 2012). The oxic-anoxic interface  
243 above oxygen minimum zones (OMZ) has been shown to provide appropriate conditions to  
244 enable N<sub>2</sub>O production (Ji et al., 2018). In the absence of oxygen, nitrate (NO<sub>3</sub><sup>-</sup>) is the next  
245 preferred electron acceptor for respiration after oxygen according to the electrochemical series  
246 (Lam and Kuypers, 2011). While nitrification is typically assumed to be an aerobic process,  
247 substantial suboxic nitrification has also been reported in many of the world ocean's major  
248 suboxic zones. Denitrification has been shown to be the dominant process for N<sub>2</sub>O production  
249 in the southern (Ji et al., 2015, 2018) and northern (Ji et al., 2018) part of the Pacific OMZ, but  
250 uncertainty still subsist: Kalvelage et al. (2013) observe that water-column denitrification was  
251 only of minor importance (<<1% total N loss) for the overall N budget in the eastern tropical  
252 South Pacific OMZ and that anammox was the dominant mode of N loss at the time of sampling.

253

254 The bacterial pool is not yet explicitly modelled in PISCES. Processes of N<sub>2</sub>O production like  
255 nitrification or denitrification are not formally expressed, and PISCES diagnoses their effects  
256 from specific environmental conditions. Such modelling approach with an indirect  
257 representation of the N<sub>2</sub>O yield is rather common in present Earth system models due to the



258 complexity of involved processes (Battaglia and Joos, 2018). For example, in MPI-ESM 1-2-LR  
259 (Ilyina et al., 2013) and MIROC-ES2L (Hajima et al., 2020), two of the few other Earth system  
260 models simulating marine N<sub>2</sub>O emissions in CMIP6 (Seferian et al., 2020), the production of  
261 N<sub>2</sub>O is mainly linked to the consumption of oxygen (O<sub>2</sub>) during remineralization of organic  
262 matter.

263  
264 In PISCES it is assumed that the distribution of nitrifying bacteria in the model is ubiquitous in  
265 the ocean interior, so wherever there is export of organic matter to depth the model computes  
266 nitrification, consuming ammonium and producing nitrate (Martinez-Rey et al., 2015).  
267 Nitrification is particularly enhanced in total absence of light, whereas oxygen levels should be  
268 above the suboxic threshold of 1 μmol L<sup>-1</sup>. Denitrification is computed in the model where  
269 dissolved oxygen concentration falls below 5 μmol L<sup>-1</sup>, which defines suboxic waters (Cocco et  
270 al., 2013; Bopp et al., 2013).

271  
272 In each grid point below 100 m depth (as N<sub>2</sub>O production is inhibited by light), a unitless  
273 function  $f(O_2)$  depending on the oxygen concentration  $[O_2]$  (in μmol L<sup>-1</sup>) is computed following:  
274

$$\left. \begin{aligned} 275 \quad f([O_2] < 1 \mu\text{mol L}^{-1}) &= [O_2] \\ 276 \quad f(1 \mu\text{mol L}^{-1} \leq [O_2] \leq 5 \mu\text{mol L}^{-1}) &= 1 \\ 277 \quad f([O_2] > 5 \mu\text{mol L}^{-1}) &= 0.7 \cdot \exp(-0.1 \cdot ([O_2] - 5)) + 0.3 \cdot \exp(-0.01 \cdot ([O_2] - 5)) \end{aligned} \right\} (1)$$

278  
279  $f(O_2)$  allows to evaluate the suboxic production of N<sub>2</sub>O based on Martinez-Rey et al. (2015):

$$280 \quad [N_2O]_{\text{suboxic}} = \alpha + \beta \cdot f(O_2) \quad (2)$$

281  
282  
283  
284 with  $\alpha$  being the nitrification coefficient for N<sub>2</sub>O background production equal to 10<sup>-4</sup> molN<sub>2</sub>O  
285 per molO<sub>2</sub> consumed.  $\beta$  is the denitrification coefficient which scales the oxygen-dependent  
286 function. It is equal to 30 · 10<sup>-4</sup> molN<sub>2</sub>O per molO<sub>2</sub> consumed.

287 Then the local trend of nitrous oxide concentration [N<sub>2</sub>O] is finally evaluated by Eq. (3) at each  
288 time step as:

$$290 \quad d[N_2O]/dt = [N_2O]_{\text{suboxic}} \cdot \text{zolimite} \cdot \text{o2ut} \quad (3.1) \text{ remineralization}$$

$$291 \quad - \text{sink}_{N_2O} \cdot [N_2O] \quad (3.2) \text{ sink term}$$

$$292 \quad + [N_2O]_{\text{suboxic}} \cdot \text{zonitr} \cdot \text{o2nit} \quad (3.3) \text{ nitrification}$$

$$293 \quad + [N_2O]_{\text{suboxic}} \cdot \text{zgrazing} \cdot \text{o2ut} \quad (3.4) \text{ grazing}$$

294  
295 where in the first term (3.1) zolimite accounts for ammonification in oxic waters through oxygen  
296 consumption during the remineralization of the organic matter at the o2ut ratio of 133/122. In  
297 the second term (3.2) sink<sub>N<sub>2</sub>O</sub> is the N<sub>2</sub>O sink term coefficient corresponding to the N<sub>2</sub>O  
298 consumed under anoxic conditions by denitrification at a rate of 7.12 · 10<sup>-4</sup> s<sup>-1</sup>. The third term  
299 (3.3) represents the part of N<sub>2</sub>O concentration produced as an intermediate product of  
300 nitrification at a o2nit ratio of 32/122. The last term (3.4) produces N<sub>2</sub>O by grazing of the  
301 remnant organic matter.

302  
303 The N<sub>2</sub>O partial pressure difference across the air-sea interface (sea-to-air Dpn<sub>2o</sub>; in atm) is  
304 then computed based on



305

$$306 \quad D_{\text{pN}_2\text{O}} = [\text{N}_2\text{O}]_{\text{surface}} / \text{solub}_{\text{N}_2\text{O}} - \text{pN}_2\text{O} * P_{\text{atm}} \quad (4)$$

307

308 with  $\text{pN}_2\text{O}$ , the atmospheric partial pressure of  $\text{N}_2\text{O}$  equal to 273.021 ppb,  $P_{\text{atm}}$  the atmospheric  
309 pressure in  $\text{N/m}^2$ , and  $\text{solub}_{\text{N}_2\text{O}}$  the  $\text{N}_2\text{O}$  solubility in  $\text{mol/m}^3$  which depends on in-situ  
310 temperature and practical salinity following the formulation of Weiss and Price (1980).

311

312 Finally sea-to-air  $\text{N}_2\text{O}$  fluxes ( $\text{mol/m}^2/\text{s}$ ) are inferred based on Wanninkhof (1992; 2014):

313

$$314 \quad \text{N}_2\text{O}_{\text{flux}} = D_{\text{pN}_2\text{O}} * \text{solub}_{\text{N}_2\text{O}} * K_{\text{gN}_2\text{O}} \quad (5)$$

315

316 with  $K_{\text{gN}_2\text{O}}$  being the piston velocity for  $\text{N}_2\text{O}$  ( $\text{m/s}$ ), which depends on wind speed, ice fraction  
317 and temperature .

318

### 319 c) Observations

320

321 Model results are compared with available observational-based gridded T/S datasets. Ocean  
322 heat content (OHC) of the upper 0-300-meters layer has been inferred from three different  
323 products: i) the global objective analysis of subsurface temperature EN4 (Good et al., 2013), ii)  
324 the SIO product of the Scripps Institution of Oceanography (Roemmich and Gilson, 2009), and  
325 iii) the ISAS20 optimal interpolation product released by the Ifremer (Kolodziejczyk et al., 2019;  
326 Kolodziejczyk et al., 2021). While SIO and ISAS20 products consider only Argo T/S profiles, EN4  
327 dataset considers all types of in situ profiles providing temperature and salinity (when  
328 available). These three in situ-based datasets are considered since 2005, when the Argo  
329 coverage became sufficient to characterize the global ocean. Details on OHC computation can  
330 be found in Llovel and Terray (2016) and Llovel et al. (2022). The text also refers to cross-  
331 validations performed on OHC of the deeper layers (0-700 m and 0-2000 m) that have been  
332 performed with OHC anomalies from World Ocean Atlas 2009 (Levitus et al., 2012). A monthly  
333 climatology (1955-2012) of oceanic temperature from World Ocean Atlas 2013 version 2  
334 (Locarnini et al., 2013) has been used to evaluate modelled temperatures. Modelled  $\text{O}_2$  has  
335 been compared with the annual climatology of  $\text{O}_2$  from World Ocean Atlas 2013 (Garcia et al.,  
336 2014). The recent dataset of  $D_{\text{pN}_2\text{O}}$  observations compiled by Yang et al. (2020) is used to  
337 evaluate modelled  $D_{\text{pN}_2\text{O}}$ .

338

## 339 3. Results

340

### 341 a) Impact of PLF on the upper ocean heat content and dynamics

342

343 Meridional sections reveal that heat perturbations in response to changing CHL fields  
344 interacting with light are limited to the top 0-300 m layer of the ocean and predominantly affect  
345 the tropical area (Figure 2 and Figure S2, c-d).





346

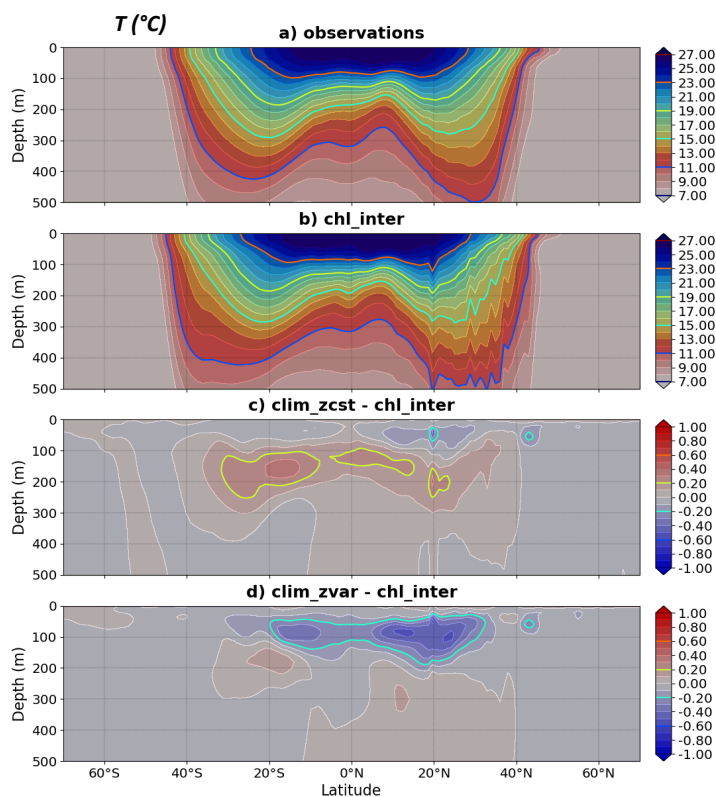


Figure 2: Mean 2009-2018 meridional section of **temperature** ( $^{\circ}\text{C}$ ) averaged over the whole tropical band ( $0\text{-}360^{\circ}\text{E}$ ) for a) observations, b) chl\_inter and its differences with c) clim\_zcst and d) clim\_zvar.

347 The largest temperature anomalies are observed near the thermocline depth and reflect upper  
348 ocean warming and deepening of the thermocline in clim\_zcst (Figure 2c), and cooling and  
349 shallowing of the thermocline in clim\_zvar (Figure 2d). In clim\_zcst the ocean warming reflects  
350 large-scale patterns of a tropical CHL deficit compared to chl\_inter (Figure S1, b). Temperature  
351 differences seen in the near-surface layer (0-50 m) is lower than that of the 50-300 m layer.  
352 This is expected as a result from weak stratification but also from experiments run with a forced  
353 atmosphere in which the temperature of the ocean surface layer is constrained by the  
354 atmospheric prescribed state.  
355  
356 When using an incomplete representation of the PLF, two contrasting trends of the upper  
357 ocean heat content (OHC) emerge compared to our control run chl\_inter (Figure 1a).  
358  
359 Over the Argo period (2005-present) EN4 estimates of tropical OHC300 are in very good  
360 agreement with our warmest experiment clim\_zcst (Figure 1b), while the two other  
361 dataproducts SIO and ISAS20 are in better agreement with our control run chl\_inter and with  
362 clim\_zvar. Note that the good accordance between modeled OHC300 and observations is not



363 to take for granted (Cheng et al., 2016; Liao et al., 2022) and that non-negligible differences  
364 among OHC dataproducts exist and are generally particularly strong in the upper 0-300 m layer  
365 (Lyman et al., 2010; Liang et al., 2021). The spread between these products at the end of the  
366 2005-2018 period ( $12.1 \cdot 10^{21}$  J) is comparable with that of our numerical set ( $13.6 \cdot 10^{21}$  J). The  
367 modelled OHC in chl\_inter is in very good agreement with current global mean in situ  
368 observations (Meysignac et al., 2019; see their Figure 11) and with OHC anomalies derived  
369 from WOA09 (Levitus et al., 2012). In accordance with these observations, our ocean-  
370 biogeochemical model simulates a global mean increase of OHC over the 2006-2016 period of  
371 order  $40 \cdot 10^{21}$  J for the upper 700 m, and of about  $70 \cdot 10^{21}$  J for the 0-2000 m layer.

372  
373 Subsurface thermal anomalies develop rapidly (Figure S3) after branching of clim\_zvar and  
374 clim\_zcst in 1999. The dipole structure of the anomaly seen in clim\_zcst reflects the surface  
375 heat trapping in chl\_inter and the associated subsurface cooling (Figure S3, b). Indeed in  
376 clim\_zcst the vertically constant and weaker profiles of CHL trap less incoming SW than the CHL  
377 maximum seen in chl\_inter between 0 and 100 m depth (Figure S1, d-f). The negative anomaly  
378 in clim\_zvar suggests that the parameterization of Morel and Berthon (1989) contributes to  
379 underestimate the ocean heat uptake (Figure S3, c and Figure S2, d) by comparison to chl\_inter.  
380 This heat deficit results from the overestimation of the vertical integral of CHL over large areas  
381 of the tropical domain in clim\_zvar compared to chl\_inter (Figure S1, c), which catch the energy  
382 associated to the incoming radiation without distributing it to the water column.

383  
384 In both clim\_zcst and clim\_zvar the subsurface temperature anomaly deepens progressively  
385 over the first six years of simulation as a result of vertical mixing (Figure S3). This evolution  
386 indicates that part of the OHC300 differences between experiments comes from the  
387 adjustment of clim\_zcst and clim\_zvar to the spin-up mean state yielded by an interactive PLF.  
388 However, differences in OHC300 from experiments having spin-ups consistent with their own  
389 PLF representations are expected to be even greater. The range of uncertainties evaluated here  
390 should be considered at the lower end of estimate of OHC discrepancies that may emerge from  
391 changing the PLF representation.

392  
393 Prescribing a constant vertical profile of CHL (clim\_zcst; green) to compute the penetration of  
394 the radiation into the ocean increases the OHC of the upper 300 meters (hereafter OHC300)  
395 by more than  $20 \cdot 10^{21}$  J during the last two decades (1999-2018) compared to chl\_inter (Figure  
396 1). This rise of OHC300 decreases the vertically-weighted sum of the tropical potential density  
397 of the upper 300 m at the end of the simulated period by  $5 \text{ kg/m}^3$  compared to chl\_inter (Figure  
398 S4). Surprisingly, the opposite trend (a reduced OHC300 compared to chl\_inter) is simulated  
399 with the same state-of-the-art CMIP6 ocean-biogeochemical model when considering a  
400 variable vertical profile of CHL (clim\_zvar; blue). However Figure 1 highlights that the simulation  
401 using a consistent CHL for interacting with both incoming SW and biogeochemical cyclings  
402 (chl\_inter) does not amplify one of these two trends, as clim\_zcst and clim\_zvar surround  
403 chl\_inter. Average ranges of uncertainties over the extended tropical domain ( $35^{\circ}\text{S}$ - $35^{\circ}\text{N}$ )  
404 exceed  $40 \cdot 10^{21}$  J in terms of OHC300 (Figure 1), 4 meters for the thermocline depth and more  
405 than  $9 \text{ kg/m}^3$  for the potential density perturbation (Figure S4).

406  
407 Similar to OHC300, ranges of uncertainty for the OHC estimates of deeper layers (0-700 m and  
408 0-2000 m) also slightly exceed  $40 \cdot 10^{21}$  J. Such uncertainty ranges are quite important as they  
409 have been obtained by only changing the PLF representation in a single ocean-biogeochemical

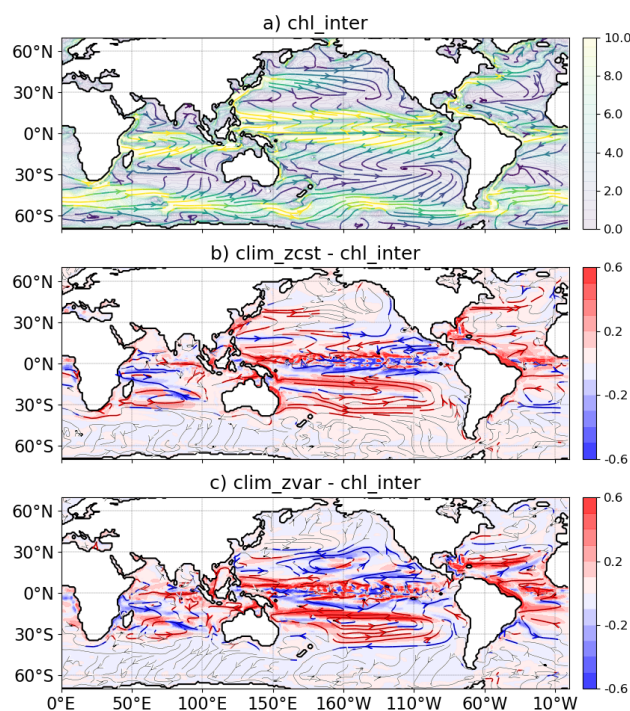


410 model. By comparison, in the context of OMIP protocols, Tsujino et al. (2020) give spreads  
411 between CMIP models estimates of order  $50 \cdot 10^{21}$  J for the OHC of the upper 700m after 20  
412 years (see their Figure 24, a-b). Regarding the OHC integrated over the 0-2000m layer, they  
413 present an inter-model spread between 50 and  $100 \cdot 10^{21}$  J, depending on the OMIP protocol  
414 considered (see their Figure 24, d-e). So, the OHC300 uncertainty of  $40 \cdot 10^{21}$  J triggered by the  
415 representation of the PLF in our set of experiments has a comparable order of magnitude than  
416 the current multi-models estimation of OHC. Part of the OHC multi-model uncertainty in  
417 current climate models may be due to different representations of the phytoplankton-light  
418 interaction.

419

420 The heat and associated density perturbations also cause dynamical modifications of upper  
421 ocean currents (Figure 3). Absolute differences in upper ocean velocities (average between 0  
422 and 300m depth) are between  $|0.05|$  and  $|0.6|$  cm/s with strongest differences along the  
423 equator revealing perturbations of the equatorial undercurrent (Figure 3, b and c). Circulation  
424 around the subtropical gyres is also impacted, in particular for the south-Pacific subtropical  
425 gyre. These modifications of zonal and meridional dynamics spread over the entire tropical  
426 latitudes, from  $30^{\circ}\text{S}$  to  $30^{\circ}\text{N}$ , strongly supporting the idea that heat perturbations induced by  
427 modifying interactions between CHL and incoming SW cause non-negligible modifications of  
428 the equatorial and tropical ocean dynamics.

429



430

431 Figure 3: Annual mean speed (color; cm/s) and streamlines of **oceanic currents** between 0-300  
432 m over the 2009-2018 period for a) chl\_inter, and its differences with b) clim\_zcst and c)  
433 clim\_zvar. In b-c) streamlines are colored when absolute speed are larger than 0.05 cm/s.



434

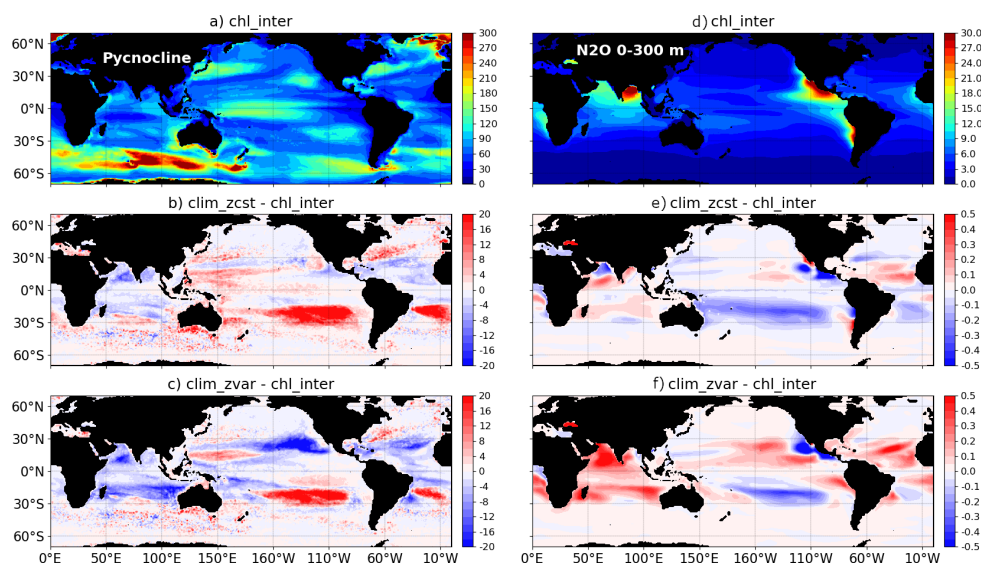
435 **b) PLF impact on N<sub>2</sub>O production**

436

437 Perturbations of the annual pycnocline depth (Figure 4, a-c) highlight a vertical adjustment to  
438 the large-scale dynamical anomalies (Figure 3). Variations of the pycnocline integrate  
439 perturbations of both thermal and salinity stratifications. However, in our experiments heat  
440 anomalies appear to drive perturbations, and pycnocline depth anomalies mainly reflect those  
441 of the thermocline. The cold anomaly dominating the tropical domain in *clim\_zvar* (Figure S2,  
442 d) appears to be vertically redistributed, as it triggers the raising of the isopycnals (Figure 4, c).  
443 In contrast to the anomalies seen over most of the tropical Pacific, a deepening of the  
444 isopycnals reaching up to 20 meters is modelled in both South Pacific and Atlantic subtropical  
445 gyres in *clim\_zcst* and *clim\_zvar* (Figure 4, b and c). Over these subtropical gyres heat is  
446 redistributed along the vertical as the subsurface warm anomaly dives which in turn causes a  
447 deepening of the pycnocline (Figure 4, b and c). As stressed by Sweeney et al. (2005), small  
448 changes in CHL concentration (Figure S1) may have important effects on the mixed layer depth  
449 in these subtropical gyres due to low local wind speeds. Strong winds would drive the mixed  
450 layer depth independently of the CHL changes, explaining why the pycnocline is barely  
451 perturbed along the equator (Figure 4, b and c). In line with their results, our set of experiments  
452 highlights that small CHL changes in low productivity regions trigger a vertical redistribution of  
453 density anomalies affecting the stratification.

454

455



456

457 Figure 4: a-c) Depth of annual **pycnocline** (m) for 2009-2018, computed as the annual mean  
458 depth of the maximum of the Brunt-Väisälä frequency  $N^2(T, S)$  over the water column (Maes  
459 and O Kane, 2014). d-f) Mean [**N<sub>2</sub>O**] (micro-molN/m<sup>3</sup>) over the first 300 meters depth for  
460 (upper line) *chl\_inter* and its mean-state differences with (middle) *clim\_zcst* and (bottom)  
461 *clim\_zvar*.

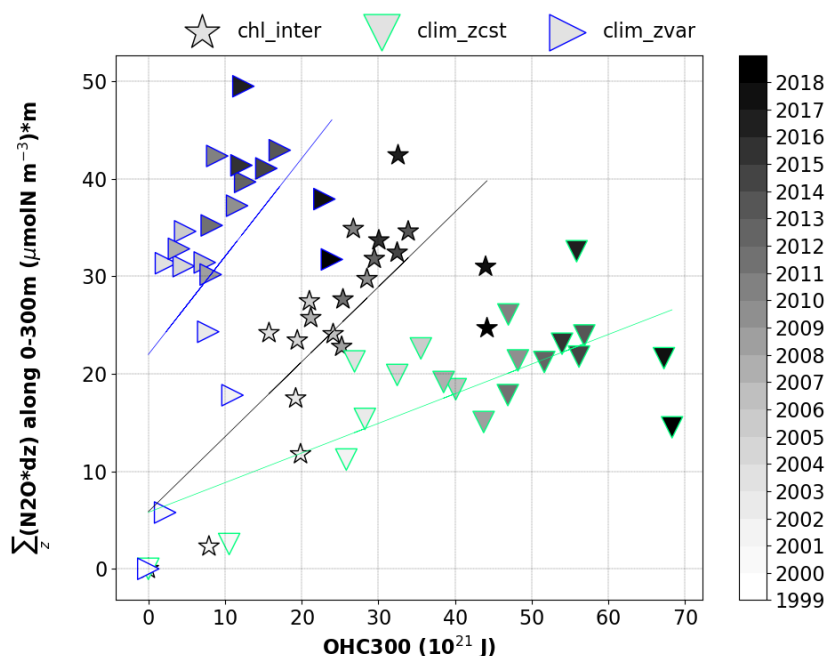
462



463 Anomalies of N<sub>2</sub>O concentration integrated over the first 300 meters of the water column  
464 (Figure 4, e and f) are in good agreement with patterns of pycnocline anomalies over the tropics  
465 (Figure 4, b and c). These comparable spatial structures attest that N<sub>2</sub>O anomalies are driven  
466 by perturbations of stratification in large parts of the tropical domain. Note that spatial patterns  
467 are robust against expanding the column used to perform the mean of N<sub>2</sub>O concentration up  
468 to 6000 meters, since most of the N<sub>2</sub>O perturbation is contained in the top 300 meters as  
469 reported also for physical variables.

470  
471 In the South Pacific subtropical gyre, the concomitance of i) an increased temperature (Figure  
472 S2, c and d), ii) a reinforced transport (Figure 3, b and c) and iii) a weakened stratification  
473 illustrated by a local deepening of the pycnocline (Figure 4, b and c), contributes to decrease  
474 the N<sub>2</sub>O concentration in both *clim\_zcst* and *clim\_zvar* (Figure 4, e and f). By contrast, in the  
475 South Indian Ocean and North tropical Atlantic the increase of N<sub>2</sub>O concentration seems to be  
476 mainly driven by the mean shoaling of the local pycnocline, as both regions exhibit contrasted  
477 perturbations in terms of transport and temperature. Finally, in the North-Pacific OMZ area,  
478 the strong N<sub>2</sub>O deficits in both *clim\_zcst* and *clim\_zvar* do not respond to stratification and  
479 transport anomalies but are rather driven by a local rise of O<sub>2</sub> concentration (Figure S5).  
480 Considering an incomplete PLF contributes to overestimate the oxygen concentration in this  
481 OMZ and leads to a lack of local N<sub>2</sub>O production.

482  
483 The relationship between N<sub>2</sub>O concentration and OHC<sub>300</sub> in the Tropical Ocean is inferred  
484 next based on the three 20-years simulations (Figure 5). Approaching the slope of the simulated  
485 distributions by a linear regression gives quite distinct tropical N<sub>2</sub>O production pathways along  
486 time as a function of the oceanic heat uptake: from 0.3 micro-molN m<sup>-2</sup> per ZJ for the most  
487 simplified PLF scenario *clim\_zcst*, to 1 micro-molN m<sup>-2</sup> per ZJ for *clim\_zvar*. The slope of the  
488 experiment with the higher level of realism in terms of interactivity (*chl\_inter*) appears a  
489 solution between the two previous extremes, as it increases its N<sub>2</sub>O production by 0.8 micro-  
490 molN m<sup>-2</sup> per ZJ. Each of these N<sub>2</sub>O production pathways will not forecast the same temporal  
491 evolution of the N<sub>2</sub>O budget and hence, the same climate in future. This result stresses the  
492 importance of having an interactive PLF in order to neither overestimate nor underestimate  
493 the N<sub>2</sub>O production forecast due to simplified representation of the PLF.  
494



495  
 496 Figure 5: Annual N<sub>2</sub>O inventory over the first 300 meters depth (micro-molN/m<sup>2</sup>/yr) as a  
 497 function of the annual OHC300 (ZJ/yr) and annually averaged over an extended tropical  
 498 domain (35°S-35°N).

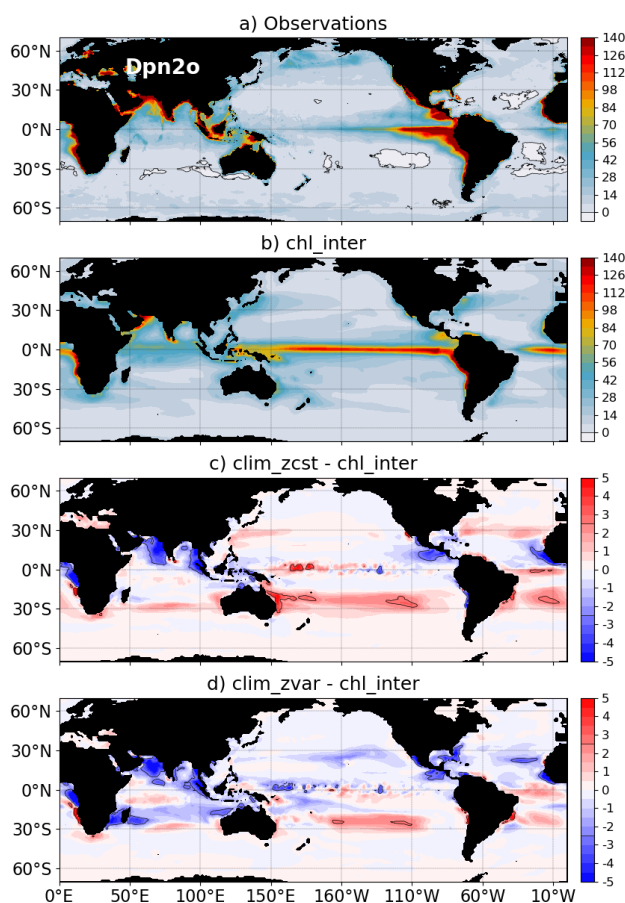
499  
 500 **d) Repercussions on oceanic N<sub>2</sub>O emissions**  
 501

502 By perturbing the OHC, the ocean dynamics and the N<sub>2</sub>O production, the degree of realism of  
 503 the PLF has non-negligible consequences on Dpn<sub>2o</sub> and thus on N<sub>2</sub>O emissions at the air-sea  
 504 interface (Figure 6). Because the atmospheric partial pressure of N<sub>2</sub>O is identical among  
 505 experiments, differences in Dpn<sub>2o</sub> are driven by differences in surface N<sub>2</sub>O concentration  
 506 normalized by those in N<sub>2</sub>O solubility. It results that spatial patterns of Dpn<sub>2o</sub> anomalies (Figure  
 507 6) reflect differences in surface N<sub>2</sub>O concentration.  
 508

509 Interestingly, compared to a scenario considering a fully interactive PLF (chl\_inter), an  
 510 incomplete representation of the PLF underestimates Dpn<sub>2o</sub> in all OMZ regions of the northern  
 511 hemisphere, which are strong emission zones (Figure 6, c and d). Large Dpn<sub>2o</sub> anomalies of -  
 512 2.5 atm encompasses northern OMZ regions of the Indian, Pacific and Atlantic oceans and  
 513 anomalies reach up to -5 natm locally. Consequently, clim\_zcst and clim\_zvar underestimate  
 514 N<sub>2</sub>O fluxes by more than 12% in these OMZ regions compared to chl\_inter. This result highlights  
 515 that the way to represent the PLF can be an important source of uncertainty in modelling N<sub>2</sub>O  
 516 fluxes. As a matter of fact, the oceanic contribution to the recent global N<sub>2</sub>O budget by Tian et  
 517 al. (2020) is based on only five global ocean-biogeochemical models (as still only few models  
 518 simulate marine N<sub>2</sub>O emissions). These models have different configurations of the PLF which  
 519 adds considerable uncertainty to simulated marine N<sub>2</sub>O emissions.  
 520



521 In subtropical gyres, the strong and direct effect of temperature (Figure S2, c and d) on [N<sub>2</sub>O]  
522 (Figure 4, e and f) is in line with Yang et al. (2020) who show that a solubility regime drives the  
523 seasonality of Dpn<sub>2</sub>o in that regions. Both clim\_zcst and clim\_zvar overestimate Dpn<sub>2</sub>o in  
524 subtropical gyres of the South Pacific and South Atlantic (Figure 6, c and d). This leads to an  
525 overestimation\_of the regional N<sub>2</sub>O fluxes by 24% compared to a simulation having a complete  
526 and interactive PLF representation (chl\_inter).  
527



528  
529 Figure 6: Mean sea-to-air **Dpn<sub>2</sub>o** (natm) computed from a) observations, b) chl\_inter over the  
530 2009-2018 period, and its differences with c) clim\_zcst and d) clim\_zvar compared to chl\_inter.

531  
532 **4. Conclusion**  
533

534 In this study we use the ocean component (including ocean physics, sea ice and marine  
535 biogeochemistry) of a global Earth system model that contributed to the last CMIP project  
536 (CMIP6). Our ocean-biogeochemical model is one of the few currently able to represent an  
537 interactive phytoplankton-light feedback (PLF) by constraining the penetration of shortwave  
538 radiation into the ocean as a function of the chlorophyll concentration produced by the



539 biogeochemical model. Three experiments have been run at the horizontal resolution currently  
540 used for intercomparisons of Earth system models ( $1^\circ$ ). Analyses are based on differences  
541 between a control run with an interactive PLF (chl\_inter) and two experiments using an  
542 incomplete PLF (clim\_zcst and clim\_zvar) characterized by the use of a prescribed CHL  
543 climatology to interact with the incoming solar radiation. Changing the way to compute how  
544 the CHL filters the light penetration into the ocean reveals specific impacts of using an  
545 interactive PLF.

546  
547 Our results show that the strategy used to account for the impact of the biology on light  
548 penetration significantly interferes with upper ocean heat uptake (Figure 1), and the associated  
549 dynamics (Figure 3) and stratification in the tropics (Figure 4, a-c). Our set of forced ocean-  
550 biogeochemical experiments reveals that marine production of nitrous oxide (N<sub>2</sub>O) is sensitive  
551 to the representation of the PLF (Figure 4, d-f). The heat perturbations add to the uncertainty  
552 of modelled oceanic N<sub>2</sub>O production, and result in three N<sub>2</sub>O production trajectories with time  
553 (Figure 5) that in turn trigger regional differences of Dpn<sub>2</sub>o and sea-air N<sub>2</sub>O fluxes (Figure 6).  
554 Compared to an ocean model using a fully interactive PLF (chl\_inter), an incomplete PLF results  
555 in an overestimation of N<sub>2</sub>O fluxes by up to 24% in the south Pacific and south Atlantic  
556 subtropical gyres, and their reduction by up to 12% in OMZ of the northern hemisphere. Our  
557 results based on a model at CMIP6 state-of-the-art emphasize an overlooked important source  
558 of uncertainty in climate projections of marine N<sub>2</sub>O production and in current estimations of  
559 the marine nitrous oxide budget.

560  
561 In subtropical gyres of the southern Hemisphere which are regions of low productivity, small  
562 CHL changes have a strong and direct effect on temperature (Figure S2, c and d), on transport  
563 (Figure 3, b and c) and on the local stratification (Figure 4, b and c). These concomitant effects  
564 result in a local decrease of the N<sub>2</sub>O concentration in both experiments having a simplified PLF  
565 representation (clim\_zcst and clim\_zvar).

566  
567 Our results also question the reliability of current modelled estimates of the area and volume  
568 of OMZ, as well as their trends in a future climate. The expansion rate of O<sub>2</sub>-depleted waters  
569 still remains unclear and its controlling mechanisms are not yet fully understood (and  
570 represented in today's models). Observations assessed that oceans have already lost around  
571 2% of the global marine oxygen since 1960 (Schmidtko et al., 2017). The expansion of OMZ is  
572 expected to result in an increase of the volume of water suitable for denitrification and to have  
573 an impact on the production and decomposition of N<sub>2</sub>O (Freing et al., 2012). Our set of  
574 experiments highlights that an incomplete representation of the PLF underestimates the  
575 expansion of oxygen-depleted waters over the 20 years of simulation in comparison to  
576 chl\_inter. In clim\_zcst and clim\_zvar the global volume (0-1000 m) of hypoxic water with [O<sub>2</sub>]  
577 under 50 mmol m<sup>-3</sup> is up to 2.3 10<sup>14</sup> m<sup>3</sup> lower in 2018 compared to that of the control run  
578 chl\_inter. Thus an incomplete representation of the PLF might lead to an underestimation by  
579 1.2 % of the modelled tropical volume of low-oxygenated waters after 20 years.

580  
581 Recent regional studies demonstrated that the interactive PLF strongly affects upwelling  
582 systems of the south Pacific and Atlantic oceans (Hernandez et al., 2017; Echevin et al., 2021).  
583 Coastal upwellings are known to be a place of high N<sub>2</sub>O production, with an annual N<sub>2</sub>O flux  
584 totting up 20% of the global fluxes while these systems occupy less than 3% of the ocean area  
585 (Yang et al., 2020). However, in our results main modelled perturbations are rather localized





586 over OMZ or subtropical gyres (Figure 4; Figure 6). While the latter regional studies have been  
587 performed using horizontal resolutions suitable to represent the complex dynamics of coastal  
588 upwellings (from 10 km to about 28 km), it is well-established that climate models resolution  
589 (~1-degree of horizontal resolution) does not allow to resolve these dynamics. The present  
590 framework was designed to evaluate the sensitivity of CMIP models to the representation of  
591 the PLF so why it used the spatial horizontal resolution of CMIP-like experiments. A step further  
592 would be to evaluate how this sensitivity depends on the horizontal resolution by running  
593 experiments at higher resolution with the same climate model. This would help to better  
594 determine how the resolution of coastal upwelling systems may impact the modelled N<sub>2</sub>O  
595 inventory through different PLF representations, as well as the associated modelled range of  
596 uncertainty.

597  
598

#### 599 Code availability

600 Sources for NEMO and PISCES codes are available from <https://forge.nemo-ocean.eu/nemo>.

601

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