

1 How does the phytoplankton-light feedback affect the marine N₂O inventory?

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10 11 **Abstract**

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13 The phytoplankton-light feedback (PLF) describes the interaction between phytoplankton
14 biomass and the downwelling shortwave radiation entering the ocean. The PLF allows to
15 simulate differential heating across the ocean water column as a function of phytoplankton
16 concentration. Only one third of the Earth system models contributing to the 6th phase of the
17 Coupled Model Intercomparison Project (CMIP6) includes a complete representation of the
18 PLF. In other models, the PLF is approximated either by a prescribed climatology of chlorophyll
19 or not represented at all. Consequences of an incomplete representation of the PLF on the
20 modelled biogeochemical state have not yet been fully assessed and remain a source of multi-
21 model uncertainty in future projection. Here, we evaluate within a coherent modelling
22 framework how representations of the PLF of varying complexity impact ocean physics and
23 ultimately marine production of nitrous oxide (N₂O), a major greenhouse gas. We exploit global
24 sensitivity simulations at 1-degree of horizontal resolution over the last two decades (1999-
25 2018) coupling ocean, sea ice and marine biogeochemistry. The representation of the PLF
26 impacts ocean heat uptake and temperature of the first 300 meters of the tropical ocean.
27 Temperature anomalies due to an incomplete PLF representation drive perturbations of ocean
28 stratification, dynamics and oxygen concentration. These perturbations translate into different
29 projection pathways for N₂O production depending on the choice of the PLF representation.
30 The oxygen concentration in the North Pacific oxygen minimum zone is overestimated in model
31 runs with an incomplete representation of the PLF which results in an underestimation of local
32 N₂O production. This leads to important regional differences of sea-to-air N₂O fluxes: fluxes are
33 enhanced by up to 24% in the south Pacific and south Atlantic subtropical gyres, but reduced
34 by up to 12% in oxygen minimum zones of the northern hemisphere. Our results based on a
35 global ocean-biogeochemical model at CMIP6 state-of-the-art shed light on current
36 uncertainties in modelled marine nitrous oxide budgets in climate models.

37 38 **Plain language summary**

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40 Phytoplankton absorbs the solar radiation entering the ocean surface, and contributes to keep
41 the associated energy in surface waters. This natural effect is either not represented in the
42 ocean component of climate models, or in a simplified manner. We show that an incomplete
43 representation of this biophysical interaction affects the way climate models simulate ocean
44 warming, which leads to uncertainties in projections of oceanic emissions of an important
45 greenhouse gas called the nitrous oxide.

47 **Key-words:** phytoplankton-light interaction; bio-physical feedback; nitrous oxide; N₂O; CMIP6
48 Earth system models; CNRM-ESM2-1; ocean-biogeochemical model; greenhouse gases; marine
49 emission; climate

50

51 **Key points:**

52 - forced ocean-biogeochemical simulations reveal that marine production of nitrous oxide is
53 sensitive to the representation of the phytoplankton-light feedback

54 - the phytoplankton-light feedback perturbs the accumulation of heat and the ocean
55 dynamics which drive changes in nitrous oxide production patterns

56 - an incomplete phytoplankton-light feedback overestimates sea-to-air N₂O fluxes by up to
57 24% in subtropical gyres and reduces them by up to 12% in oxygen minimum zones

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60 **1. Introduction**

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62 Feedbacks between the physical, biogeochemical, or ecosystem components of the ocean can
63 trigger abrupt system changes (Heinze et al., 2021). At present the interactive phytoplankton-
64 light feedback (PLF) is the only coupling in Earth system models between modelled marine
65 biogeochemistry and ocean dynamics (Séférian et al., 2020). It implies that the chlorophyll
66 (CHL) produced by the biogeochemical model is used to determine the fraction of shortwave
67 radiation penetrating ocean surface waters. In this case, the CHL concentration profile used to
68 approximate the influence of plankton biomass on the vertical redistribution of heat in the
69 upper ocean is consistent with the one used to compute biogeochemical cycling.

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

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73 Since the first observational evidence on how suspended matter in surface waters will impact
74 light absorption by the ocean and change the radiative imbalance within the mixed layer (Kahru
75 et al. 1993), this biophysical interaction has been gradually included to ocean models. Gildor
76 and Naik (2005) highlighted the importance of considering monthly variations of CHL to capture
77 the first-order effect of marine biota on light penetration in ocean models. Adding light-CHL
78 interactions to numerical simulations affects oceanic processes over a wide range of spatial and
79 temporal scales. Enabling a phytoplankton-light interaction modifies the hydrodynamics of the
80 water column (Edwards et al., 2001; Edwards et al., 2004), the intensity of the spring-bloom in
81 subpolar regions (Oschlies, 2004), the maintenance of the Pacific Cold Tongue (Anderson et al.,
82 2007), the seasonality of the Arctic Ocean (Lengaigne et al., 2009), the strength of the tropical
83 Pacific annual cycle, as well as the ENSO variability (Timmermann and Jin, 2002; Marzeion et
84 al., 2005), the northward extension of the meridional overturning circulation (Patara et al.,
85 2012) and the cooling of the Atlantic and Peru-Chili upwelling systems (Hernandez et al., 2017,
86 Echevin et al., 2022).

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88 However, the mean effect of the PLF on sea surface temperature has been argued to depend
89 on the numerical framework (forced ocean versus coupled ocean-atmosphere models). The
90 conflicting results reported in the literature were mainly due to diverging bio-optical protocols
91 among models rather than to the inclusion of air-sea coupling. According to Park et al. (2014)
92 atmosphere-ocean coupling amplifies the magnitude of PLF-induced changes, without altering
93 the sign of the response obtained in ocean-only simulations. Two main causes were put forward

94 to explain the sign of the final heat perturbation: either an indirect dynamical response
95 (Murtugudde et al., 2002; Löptien et al., 2009) or a direct thermal effect (Mignot et al., 2013;
96 Hernandez et al., 2017). Hernandez et al. (2017) further distinguished a local from a remote
97 thermal effect by highlighting the important role played by the advection of offshore CHL-
98 induced cold anomalies in the Benguela upwelling waters. The interplay of these mechanisms
99 is regionally variable (Park et al., 2014). Despite the diversity of modelled responses, a
100 consensus emerges on the first order effect of PLF on the ocean physics, which is to perturb
101 the ocean thermal structure (Nakamoto et al., 2001; Murtuggude et al., 2002; Oeschies, 2004;
102 Manizza et al., 2005, 2008; Anderson et al., 2007; Lengaigne et al., 2007; Gnanadesikan and
103 Anderson, 2009; Löptien et al., 2009; Patara et al., 2012; Mignot et al., 2013; Hernandez et al.,
104 2017). By trapping more heat at the ocean surface in eutrophic regions, such as coastal or
105 equatorial upwellings areas, the presence of phytoplankton initially increases the surface
106 warming. Confining heat at the surface leads to less heat penetrating in subsurface. In some
107 cases, the advection and upwelling of subsurface cold anomalies can lead to remote cooling
108 effects (Hernandez et al., 2017; Echevin et al., 2022). Dynamical readjustment in response to
109 perturbations in thermal structure has also been shown to have a cooling effect, by increasing
110 upwelling of cold water to the ocean surface (Manizza et al. 2005; Marzeion et al., 2005;
111 Nakamoto et al., 2001; Löptien et al., 2009; Lengaigne et al., 2007; Park et al., 2014). Because
112 these effects depend on upper ocean stratification, an important role is attributed to modelled
113 seasonal deepening of the mixed layer as it determines the intensity of the underlying
114 temperature anomaly and its vertical movement to the surface. In other terms, whatever the
115 temporality of the causal chain, changes in the PLF representation are expected to both perturb
116 the ocean heat uptake, and trigger perturbations of both the water column stratification and
117 associated ocean dynamics.

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119 **b) This study: implications for N₂O budget uncertainties**

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121 Nitrous oxide (N₂O) is a major ozone-depleting substance (Ravishankara et al., 2009; Freing et
122 al., 2012) and a potent greenhouse gas, whose global warming potential is 265-298 times that
123 of CO₂ for a 100-year timescale (Myhre et al., 2013). The spatial coherence between marine
124 productive areas and observed hot-spots of N₂O production leads to question the impact of an
125 incomplete representation of the PLF on the simulated N₂O inventory. Recent observational
126 studies highlight that N₂O production is high in low-oxygen tropical regions and cold upwelling
127 waters (Arévalo-Martínez et al. 2018; 2020; Yang et al., 2020; Wilson et al., 2020). N₂O becomes
128 increasingly saturated in surface waters of equatorial upwelling regions due to the upward
129 advection of N₂O-rich waters (Arévalo-Martínez et al., 2017). Regions known to account for the
130 most productive areas of the ocean spatially coincide with highest N₂O production: 64% of the
131 annual N₂O flux occurs in the tropics, and 20% in coastal upwelling systems that occupy less
132 than 3% of the ocean area (Yang et al., 2020).

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134 Despite recent advances, a large range of uncertainties still surrounds oceanic N₂O emissions
135 as large areas of both the open and coastal ocean remain undersampled by observations
136 (Wilson et al., 2020). In particular, the paucity of observational data over key source regions
137 contributes to increase uncertainties. The recent global budget of Tian et al. (2020) estimates
138 natural sources from soils and oceans to contribute with up to 57% to the total N₂O emissions
139 between 2007 and 2016, with the ocean flux reaching 3.4 (2.5–4.3) Tg N yr⁻¹. A large uncertainty
140 range is associated to the ocean flux estimate, as it is based on outputs from only a small

141 number of global ocean-biogeochemical models. Very few climate models, even in the current
142 CMIP6 generation, include emissions (and beforehand a complete representation of N cycling)
143 of N₂O fluxes: only 4 out of the 26 Earth system models considered in S  f  rian et al. (2020)
144 simulate marine N₂O emissions.

145
146 The last generation of Earth system models projects an enhanced ocean warming in response
147 to climate change, which is in turn expected to increase upper-ocean stratification (Sall  e et
148 al., 2021) and to contribute to greater reductions in upper-ocean nitrate and subsurface oxygen
149 ventilation (Kwiatkowski et al., 2020). Ocean warming and deoxygenation constitute two
150 triggers of high-probability high-impact climate tipping points (Heinze et al., 2021) and are
151 identified as two of the main environmental factors influencing marine N₂O distributions (IPCC,
152 2019; Hutchins and Capone, 2022). Through its expected impacts on the upper ocean
153 stratification, the PLF representation could further change the oceanic N₂O source by
154 modulating the mixing between N₂O-rich water and intermediate depths, perturbing the way
155 N₂O-rich water reaches the air-sea interface (Freing et al., 2012).

156
157 Here we investigate how an incomplete representation of the PLF leads to uncertainties in N₂O
158 projection in an up-to-date global ocean-biogeochemical model making up the current
159 generation of Earth system models. Section 2 describes the numerical model and the set of
160 simulations, as well as the existing options to consider CHL modulations of the incoming
161 shortwave radiation. Section 3 presents the effect of an interactive PLF on the ocean heat
162 content, associated ocean stratification and dynamics, and its feedback on marine N₂O
163 inventory. Finally, Section 4 summarizes the main results, addresses their broader implications,
164 and discusses the future work motivated by this study.

165 166 **2. Methodology**

167 168 **a) Configuration of the global ocean-biogeochemical model**

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170 Recent projections of future N₂O emissions contributing to intercomparison projects like CMIP6
171 are still based on Earth system models with a low spatial resolution (S  f  rian et al., 2020). For
172 sake of coherence with CMIP biogeochemical modelling efforts, in the following we use a global
173 ocean-biogeochemical configuration of the NEMO-PISCESv2 model (Madec, 2008; Aumont et
174 al., 2015) at 1   of horizontal resolution. This model corresponds to the oceanic component of
175 CNRM-ESM2-1 (S  f  rian et al., 2019) and is one of the few CMIP6-class models that contributed
176 to the Global N₂O budget (Tian et al., 2020). Our modelled ocean has 75 vertical levels and the
177 first level is at 0.5 meter depth. Vertical levels are unevenly spaced with 35 levels being in the
178 first 300 meters of depth. Atmospheric forcings of momentum, incoming radiation,
179 temperature, humidity, and freshwater are provided to the ocean surface by bulk formulae
180 following Large and Yeager (2009). Details on physical configuration are given in Berthet et al.
181 (2019). Using an ocean-only configuration allows to isolate the local response induced by the
182 PLF by not confounding it with potential inter-basin feedbacks acting through the atmosphere.

183
184 JRA55-do atmospheric reanalysis (Tsuji  no et al., 2018; Tsuji  no et al., 2020) provided the
185 atmospheric forcings of the ocean. The global domain was first spun-up under preindustrial
186 conditions during several hundred years ensuring that all fields approached a quasi-steady
187 state. The historical evolution of atmospheric CO₂ and N₂O concentrations was prescribed since

188 1850. To avoid the warming jump between the end of the spin-up and the onset of the
189 reanalyses in 1958, the first 5 years of JRA55-do forcings were cycled, followed by the complete
190 period of JRA55-do atmospheric forcing from 1958 to 2018.

191
192 **b) Experimental design: three representations of the PLF**

193
194 The control simulation (hereafter REF) together with the spin-up both account for a fully
195 interactive PLF: the penetration of shortwave radiation into the ocean surface is constrained
196 by the CHL concentration ([CHL]) produced by the PISCESv2 biogeochemical component (Figure
197 S1, REF).

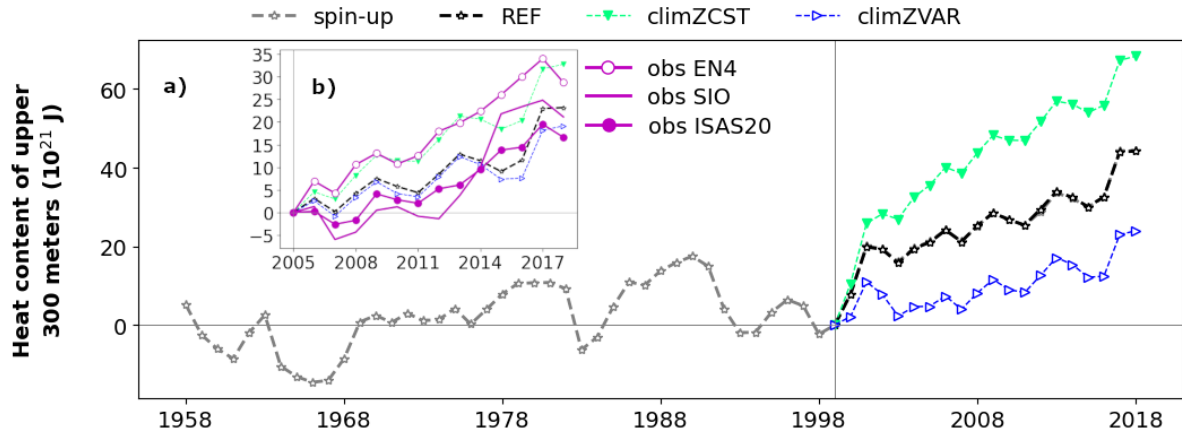
198
199 PISCESv2 (Pelagic Interactions Scheme for Carbon and Ecosystem Studies v2) is a 3D
200 biogeochemical model which simulates the lower trophic levels of marine ecosystems
201 (nanophytoplankton, diatoms, microzooplankton and mesozooplankton), the biogeochemical
202 cycles of carbon and of the main nutrients (phosphate, nitrogen, iron, and silicate) along the
203 75 levels of our numerical ocean. A comprehensive presentation of the model is found in
204 Aumont et al. (2015). PISCESv2 simulates prognostic 3D distributions of nanophytoplankton
205 and diatom concentrations. The evolution of phytoplankton biomasses is the net outcome of
206 growth, mortality, aggregation and grazing by zooplankton. Growth rate of phytoplankton
207 mainly depends on the length of the day, depths of the mixed layer and of the euphotic zone,
208 the mean residence time of the cells within the unlit part of the mixed layer and includes a
209 generic temperature dependency (Eppley, 1972). Nanophytoplankton growth depends on the
210 external nutrient concentrations in nitrogen and phosphate (Monod-like parameterizations of
211 N and P limitations), and on Fe limitation which is modeled according to a classical quota
212 approach. The production terms for diatoms are defined as for nanophytoplankton, except that
213 the limitation terms also include silicate.

214
215 Light absorption by phytoplankton depends on the waveband and on the species (Bricaud et
216 al., 1995). A simplified formulation of light absorption by the ocean is used in our experiments
217 to calculate both the phytoplankton light limitation in PISCESv2 and the oceanic heating rate
218 (Lengaigne et al., 2007). In this formulation, visible light is split into three wavebands: blue
219 (400–500 nm), green (500–600 nm) and red (600–700 nm); for each waveband, the CHL-
220 dependent attenuation coefficients, k_R , k_G and k_B , are derived from the formulation proposed
221 in Morel and Maritorena (2001):

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223
$$k_{WLB} = \sum_{\lambda_1}^{\lambda_2} (k(\lambda) + \chi(\lambda)[\text{CHL}]^{e(\lambda)}) \quad (1)$$

224 where WLB means the wavelength band associated to red (R), green (G) or blue (B), and
225 bounded by the wavelengths λ_1 and λ_2 as detailed above. $k(\lambda)$ is the attenuation coefficient
226 for optically pure sea water. $\chi(\lambda)$ and $e(\lambda)$ are fitted coefficients which allows to determine
227 the attenuation coefficients due to chlorophyll pigments in sea water (Morel and Maritorena,
228 2001).

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230
 231 Figure 1: Modelled tropical [35°S-35°N] heat content of upper 300 m (OHC300; in ZJ) for each
 232 simulation described in Table 1: REF (black; empty stars), climZCST (green; full downward
 233 triangles) and climZVAR (blue; empty rightward triangles). In (a) final part of the spin-up has
 234 been added in gray to illustrate the branching protocol in year 1999, and OHC300 anomalies
 235 have been computed with respect to year 1999. Subplot (b) zooms over the Argo period to
 236 compare modelled tropical OHC300 anomalies with 3 in situ-based products (see section 2c).
 237

238 At year 1999 two sensitivity experiments were branched off (Figure 1). Both simulations
 239 climZCST and climZVAR account for an incomplete and external PLF, as they consider an
 240 observed climatology of surface [CHL] from ESACCI (Valente et al., 2016) in order to compute
 241 the light penetration into sea water (Equation 1; Figure S1). These two simulations differ from
 242 each other by the "realism" of the vertical profile derived in each grid point from the surface
 243 value of the ESACCI CHL climatology to the level of light extinction (Table 1). climZCST uses
 244 constant profiles of CHL spreading uniformly in the vertical direction (Figure 2, b and d-f).
 245 climZVAR uses variable vertical profiles computed following Morel and Berthon (1989) (Figure
 246 2, c and d-f). This set of simulations is representative of the several configurations used in the
 247 case of CMIP intercomparison project.
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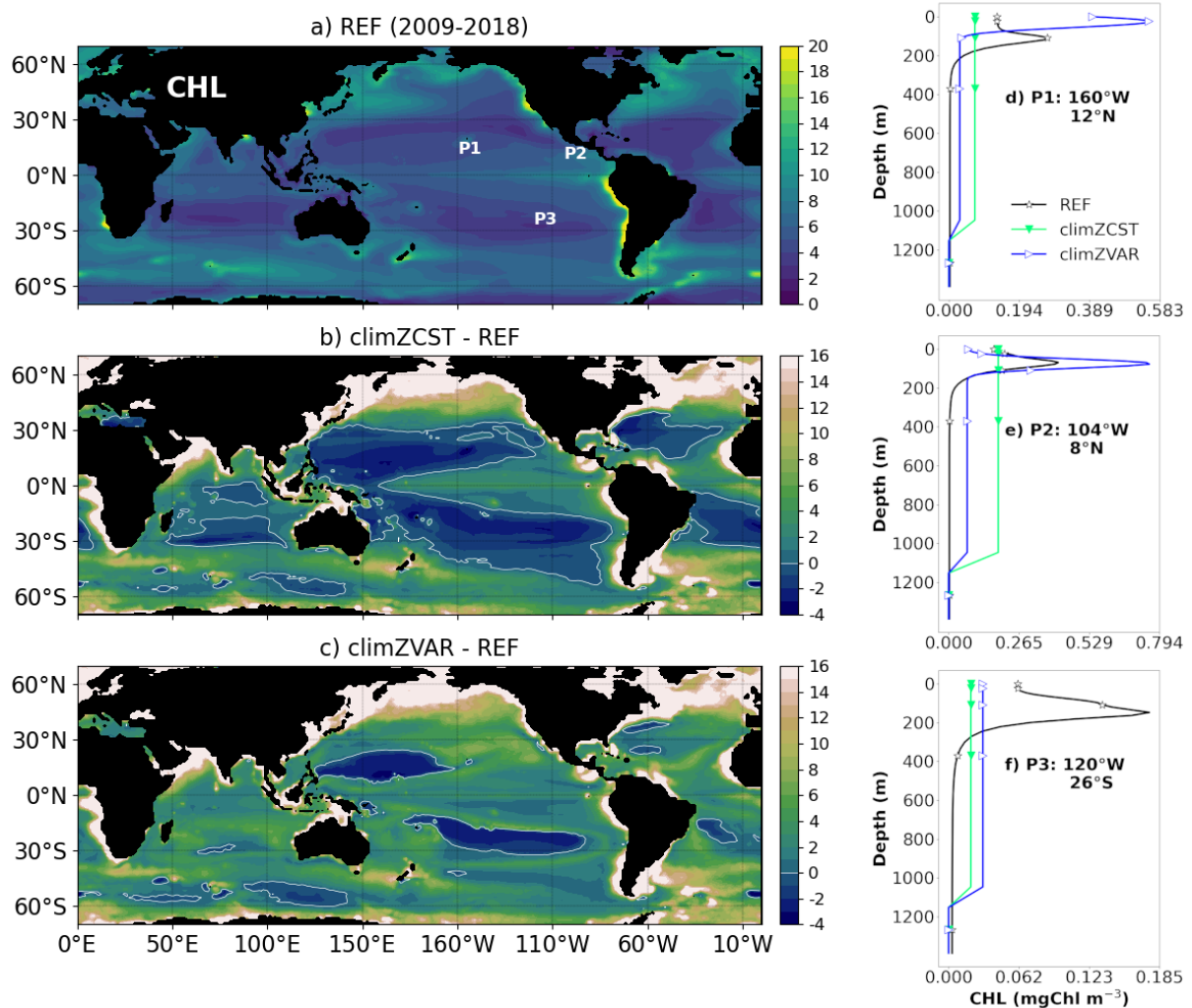
249 Table 1: Experimental set-up.
 250

Simulation	Which CHL fields to interact with incoming shortwave radiation?	PLF nature
REF	uses directly the 3D CHL produced by the biogeochemical component	interactive
climZCST	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
climZVAR	uses the prescribed monthly climatology of ESACCI CHL with a variable vertical profile, derived from the surface climatology following Morel and Berthon (1989)	incomplete

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253 In climZCST and climZVAR, PISCESv2 prognostically simulates [CHL], a key component of
 254 biogeochemical cycles, but feedback of CHL on physics (stratification, ocean heat content) is
 255 determined by the externally prescribed [CHL] climatology. The CHL concentrations used for
 256 radiation or for biogeochemical cycles are not consistent, and phytoplankton biomass
 257 computed by the biogeochemical model does not affect the physical properties of the ocean
 258 waters.

259
 260 Consequences on the marine biogeochemical mean state of incomplete representations of the
 261 PLF are assessed in the following by difference to the control run REF. This methodology allows
 262 to evaluate how different levels of realism and complexity in resolving bio-physical interactions
 263 impact the physical and biogeochemical content of the modelled ocean. A complete
 264 description of the marine N₂O parameterization used in this model is presented in the
 265 supplementary material.



266
 267 Figure 2: CHL concentration (mgCHL m^{-3}) interacting with the incoming shortwave radiation for
 268 each numerical experiment (Table 1). Maps a-c) show annual means of the vertical sum over 0-
 269 6000 m, a) as modelled over the 2009-2018 period for REF, and its differences with the external
 270 CHL prescribed for b) climZCST and c) climZVAR experiments. Labels P1 to P3 on subplot a)
 271 locate vertical profiles shown on subplots d-f).

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c) Observations and analyses

Model results are compared with available observational-based gridded temperature and salinity datasets. Ocean heat content (OHC) of the upper 0-300 meter layer was inferred from three different products: i) the global objective analysis of subsurface temperature EN4 (Good et al., 2013), ii) the SIO product of the Scripps Institution of Oceanography (Roemmich and Gilson, 2009), and iii) the ISAS20 optimal interpolation product released by Ifremer (Kolodziejczyk et al., 2019; Kolodziejczyk et al., 2021). While the SIO and ISAS20 products consider only Argo temperature and salinity profiles, the EN4 dataset considers all types of *in situ* profiles providing temperature and salinity (when available). These three *in situ*-based datasets are considered since 2005, the year the Argo coverage became sufficient to characterize the global ocean. Details on OHC computation are given in Llovel and Terray (2016) and Llovel et al. (2022). The authors also refer to cross-validations of OHC of deeper layers (0-700 m and 0-2000 m) against OHC anomalies from World Ocean Atlas 2009 (Levitus et al., 2012). A monthly climatology (1955-2012) of oceanic temperature from World Ocean Atlas 2013 version 2 (Locarnini et al., 2013) was used to evaluate modelled temperatures. Modelled O₂ was compared to the annual climatology of O₂ from World Ocean Atlas 2013 (Garcia et al., 2014) and modelled CHL was compared to the 3D monthly climatological global product estimated from merged satellite and hydrological data of Uitz et al. (2006). Modelled N₂O partial pressure difference across the air-sea interface (Dpn2o) was compared to the recent dataset of Dpn2o observations compiled by Yang et al. (2020).

In the following temporal means cover the last 10 years of simulations, from 2009 to 2018. In other analyses the whole simulated period is shown (1999-2018).

3. Results

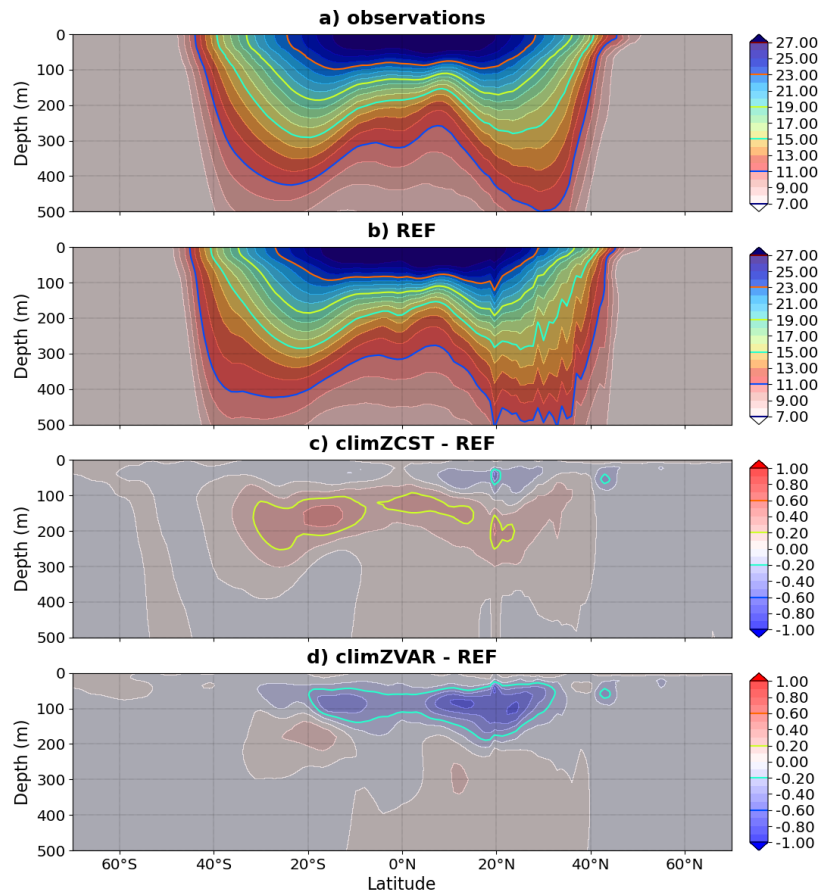
a) Impact of PLF on the upper ocean heat content and dynamics

Meridional sections reveal that heat perturbations in response to changing CHL fields interacting with light are limited to the top 0-300 m layer of the ocean and predominantly affect the tropical area (Figure 3 and Figure S2, c-d).

The largest temperature anomalies are observed near the thermocline depth and reflect upper ocean warming and deepening of the thermocline in climZCST (Figure 3c), and cooling and shallowing of the thermocline in climZVAR (Figure 3d). In climZCST the ocean warming reflects large-scale patterns of a tropical CHL deficit compared to REF (Figure 2, b). Temperature differences are lower in the near-surface layer (0-50 m) than in the 50-300 m layer. This is expected as a result from weak stratification but also from simulations run with a forced atmosphere in which the temperature of the ocean surface layer is constrained by the atmospheric prescribed state.

When using an incomplete representation of the PLF, two contrasting trends of the upper ocean heat content (OHC) emerge compared to our control run REF (Figure 1a). Over the Argo period (2005-present) EN4 estimates of tropical OHC300 are in very good agreement with our warmest simulation climZCST (Figure 1b), while the two other dataproducts SIO and ISAS20 are

320 in better agreement with our control run REF and with climZVAR. The good accordance
 321 between modeled OHC300 and observations is not a systematic feature of model-data
 322 comparisons (Cheng et al., 2016; Liao et al., 2022). Moreover, non-negligible differences exist
 323 among OHC dataproducts which are generally particularly strong in the upper 0-300 m layer
 324 (Lyman et al., 2010; Liang et al., 2021). The spread between these products at the end of the
 325 2005-2018 period ($12.1 \cdot 10^{21}$ J) is comparable to that of our numerical set ($13.6 \cdot 10^{21}$ J). The
 326 modelled OHC in REF is in very good agreement with current global mean *in situ* observations
 327 (Meysignac et al., 2019; see their Figure 11) and with OHC anomalies derived from World
 328 Ocean Atlas 2009 (Levitus et al., 2012). In accordance with these observations, our ocean-
 329 biogeochemical model simulates a global mean increase of OHC over the 2006-2016 period of
 330 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.
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Figure 3: Mean 2009-2018 meridional section of temperature ($^{\circ}\text{C}$) averaged over 0-360 $^{\circ}\text{E}$ for
 a) observations, b) REF and its differences with c) climZCST and d) climZVAR.

334 Subsurface thermal anomalies develop rapidly (Figure S3) after branching of climZVAR and
 335 climZCST in 1999. The dipole structure of the anomaly seen in climZCST reflects the surface
 336 heat trapping in REF and the associated subsurface cooling (Figure S3, b). Indeed in climZCST
 337 the vertically constant and weaker concentrations of CHL trap less incoming shortwave than
 338 the CHL maximum seen in REF between 0 and 100 m depth (Figure 2, d-f). The negative anomaly
 339 in climZVAR suggests that the parameterization of Morel and Berthon (1989) contributes to
 340 underestimate the ocean heat uptake (Figure S3, c and Figure S2, d) compared to REF. This heat
 341 deficit results from the overestimation of the vertical integral of CHL over large areas of the

342 tropical domain in climZVAR compared to REF (Figure 2, c). As a result, the energy associated
343 with the incoming radiation is caught in surface waters without being distributed over the water
344 column.

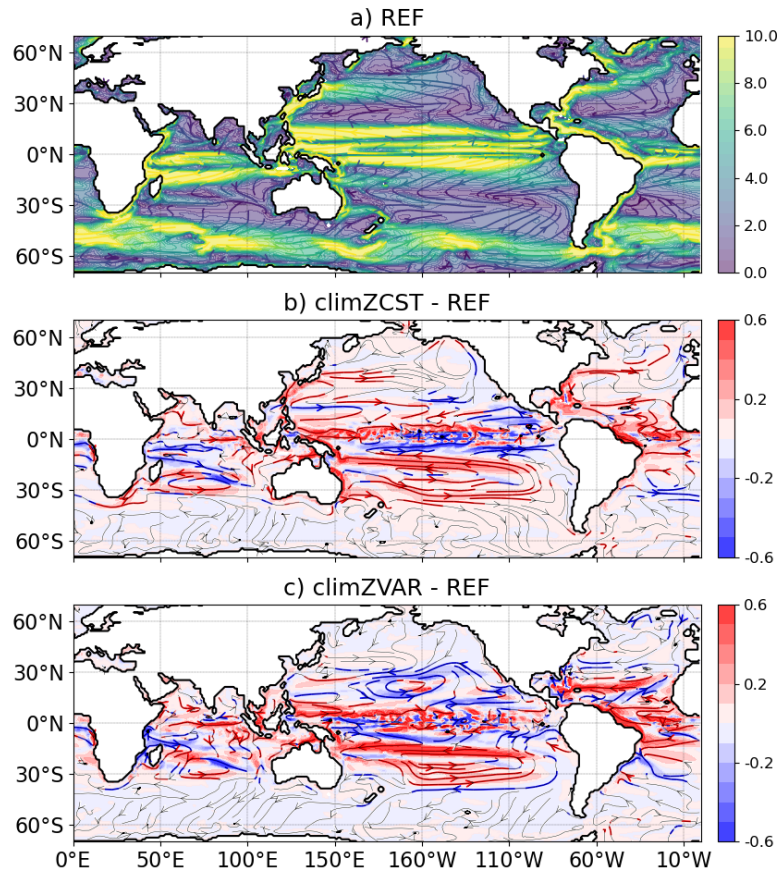
345
346 In both climZCST and climZVAR the subsurface temperature anomaly deepens progressively
347 over the first six years of simulation as a result of vertical mixing (Figure S3). This evolution
348 indicates that part of the OHC300 differences between simulations comes from the adjustment
349 of climZCST and climZVAR to the spin-up mean state yielded by an interactive PLF. It can be
350 expected that experiments having spin-ups run with different representations of the PLF, would
351 give even stronger sensitivities than those highlighted in this study. The sensitivities of OHC300
352 to the PLF formulation evaluated here should be considered at the lower end of estimate of
353 OHC discrepancies that may emerge from changing the PLF representation.

354
355 Prescribing a constant vertical profile of CHL (climZCST) to compute the penetration of the
356 radiation into the ocean increases the OHC300 by more than $20 \cdot 10^{21}$ J during the last two
357 decades (1999-2018) compared to REF (Figure 1). This rise of OHC300 decreases the vertically-
358 integrated tropical potential density of the upper 300 m at the end of the simulated period by
359 5 kg/m^2 compared to REF (Figure S4). The opposite trend (a reduced OHC300 compared to REF)
360 is simulated with the same state-of-the-art CMIP6 ocean-biogeochemical model when
361 considering a variable vertical profile of CHL (climZVAR). However Figure 1 highlights that the
362 simulation using a consistent CHL for interacting with both incoming shortwave radiation and
363 biogeochemical cyclings (REF) does not amplify one of these two trends, as climZCST and
364 climZVAR surround REF. Average ranges of uncertainties associated with the PLF
365 representation over the extended tropical domain (35°S - 35°N) exceed $40 \cdot 10^{21}$ J in terms of
366 OHC300 (Figure 1), 4 meters for the thermocline depth and more than 9 kg/m^2 for the
367 vertically-integrated potential density perturbation (Figure S4).

368
369 Similar to OHC300, ranges of uncertainty for the OHC estimates of deeper layers (0-700 m and
370 0-2000 m) also slightly exceed $40 \cdot 10^{21}$ J. Such uncertainty ranges are quite important as they
371 are obtained by only changing the PLF representation in a single ocean-biogeochemical model.
372 By comparison and in the context of OMIP protocols, Tsujino et al. (2020) give spreads between
373 CMIP model estimates of the order of $50 \cdot 10^{21}$ J for the OHC of the upper 700m after 20 years
374 (please refer to their Figure 24, a-b). Regarding the OHC integrated over the 0-2000m layer,
375 they report an inter-model spread between 50 and $100 \cdot 10^{21}$ J, depending on the OMIP protocol
376 considered (see their Figure 24, d-e). The OHC300 uncertainty of $40 \cdot 10^{21}$ J triggered by the
377 representation of the PLF in our set of simulations has a comparable order of magnitude than
378 the current spread of multi-model estimations of OHC. The present study suggests that part of
379 the OHC multi-model uncertainty in current climate models may be due to different
380 representations of the phytoplankton-light interaction.

381
382 The heat and associated density perturbations also cause dynamical modifications of upper
383 ocean currents (Figure 4). Absolute differences in upper ocean velocities (average between 0
384 and 300m depth) are between $|0.05|$ and $|0.6|$ cm/s with strongest differences along the
385 equator revealing perturbations of the equatorial undercurrent (Figure 4, b and c). Circulation
386 around the subtropical gyres is also impacted, in particular for the South Pacific subtropical
387 gyre. These modifications of zonal and meridional dynamics spread over the entire tropical
388 latitudes, from 30°S to 30°N , strongly supporting the idea that heat perturbations induced by

389 different interactions between CHL and incoming shortwave cause non-negligible
 390 modifications of the equatorial and tropical ocean dynamics.
 391

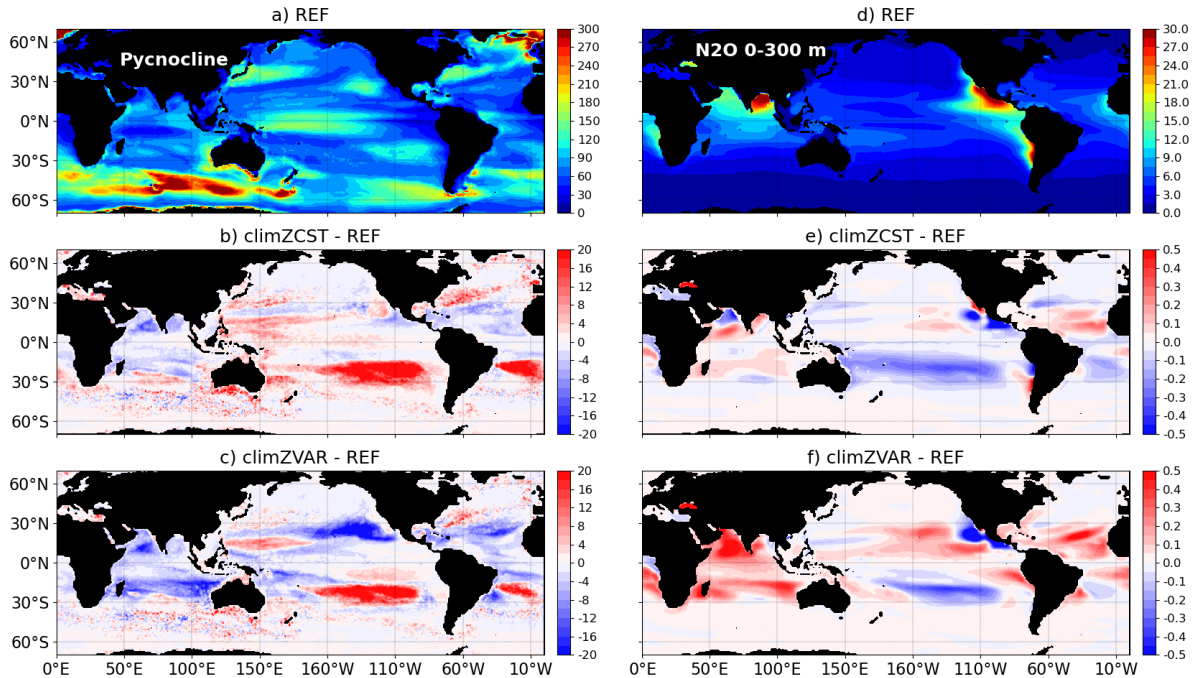


392
 393 Figure 4: Annual mean speed (color; cm/s) and streamlines of oceanic currents between 0-300
 394 m over the 2009-2018 period for a) REF, and its differences with b) climZCST and c) climZVAR.
 395 In b-c) streamlines are colored when absolute speed are larger than 0.05 cm/s.

396
 397 **b) PLF impact on N₂O production**
 398

399 Perturbations of the annual pycnocline depth (Figure 5, a-c) highlight a vertical adjustment to
 400 the heat (Figure S2) and subsequent large-scale dynamical anomalies (Figure 4). Variations of
 401 the pycnocline integrate perturbations of both thermal and salinity stratifications. However, in
 402 our simulations heat anomalies appear to drive perturbations and pycnocline depth anomalies
 403 mainly reflect those of the thermocline. The cold anomaly dominating the tropical domain in
 404 climZVAR (Figure S2, d) appears to be vertically redistributed, as it triggers an upward
 405 displacement of the isopycnals (Figure 5, c). In contrast to the anomalies seen over most of the
 406 tropical Pacific, a deepening of the isopycnals reaching up to 20 meters is modelled in both
 407 South Pacific and Atlantic subtropical gyres in climZCST and climZVAR (Figure 5, b and c). Over
 408 these subtropical gyres heat is redistributed along the vertical as the subsurface warm anomaly
 409 dives. The subduction of these heat anomalies causes in turn a deepening of the pycnocline
 410 (Figure 5, b and c). As stressed by Sweeney et al. (2005), small changes in CHL concentration
 411 (Figure S5) may have important effects on the mixed layer depth in these subtropical gyres due
 412 to low local wind speeds and low mixing conditions. This is thought to explain the large
 413 sensitivity we observe in terms of pycnocline depth (Figure 5) and ocean heat content in these

414 regions. In line with their results, our set of simulations highlights that small CHL changes in low
 415 productivity regions trigger a vertical redistribution of density anomalies affecting the
 416 stratification.
 417
 418



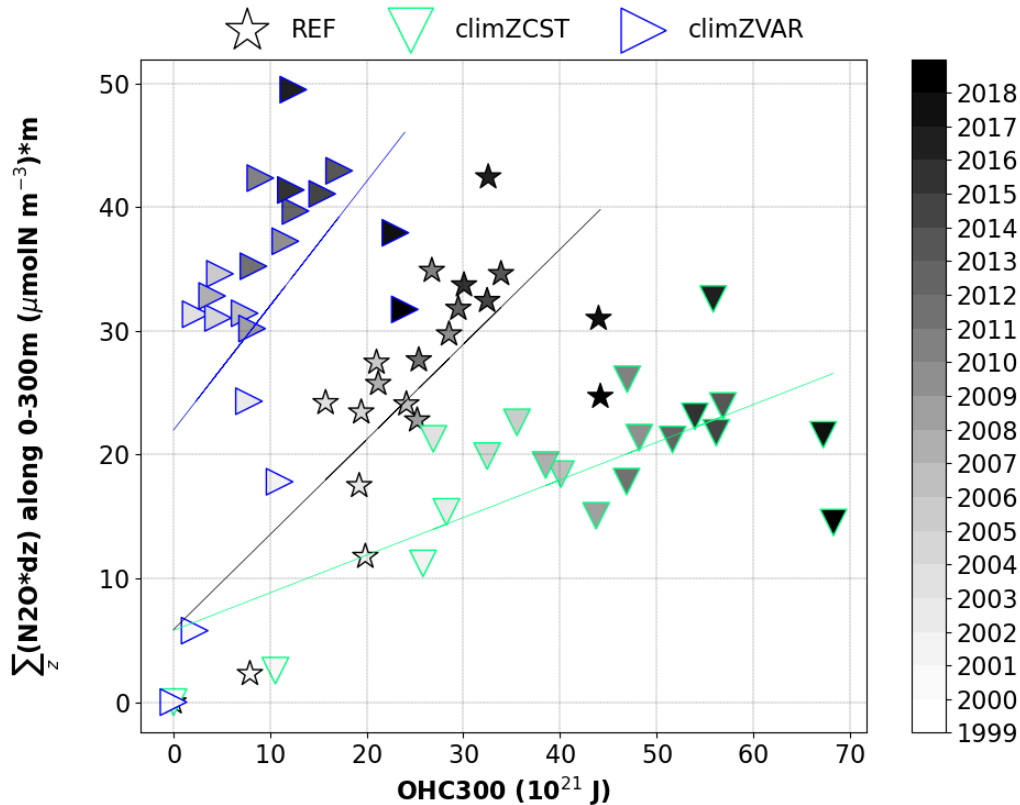
419 Figure 5: a-c) Depth of annual pycnocline (m) for 2009-2018 computed as the annual mean
 420 depth of the maximum of the Brunt-Väisälä frequency $N^2(T, S)$ over the water column (Maes
 421 and O Kane, 2014). d-f) Mean $[N_2O]$ ($\mu\text{molN}/\text{m}^3$) over the first 300 meters depth. For REF (upper
 422 panel) and its mean-state differences with climZCST (middle panel) and climZVAR (bottom
 423 panel).
 424
 425

426 Anomalies of N_2O concentration integrated over the first 300 meters of the water column
 427 (Figure 5, e and f) are in good agreement with patterns of pycnocline anomalies over the tropics
 428 (Figure 5, b and c). These comparable spatial structures attest that N_2O anomalies are driven
 429 by perturbations of stratification in large parts of the tropical domain.
 430

431 In the South Pacific subtropical gyre, the concomitance of i) an increased temperature (Figure
 432 S2, c and d), ii) a reinforced transport (Figure 4, b and c) and iii) a weakened stratification
 433 illustrated by a local deepening of the pycnocline (Figure 5, b and c), contributes to decrease
 434 the N_2O concentration in both climZCST and climZVAR (Figure 5, e and f). In contrast, in the
 435 South Indian Ocean and North tropical Atlantic the increase of N_2O concentration seems to be
 436 mainly driven by the mean shoaling of the local pycnocline, as both regions exhibit contrasted
 437 perturbations in terms of transport and temperature. Finally, in the North Pacific oxygen
 438 minimum zone, the strong N_2O deficits in both climZCST and climZVAR compared to REF do not
 439 respond to stratification and transport anomalies but are rather driven by a local rise of O_2
 440 concentration (Figure S6). Considering an incomplete PLF contributes to overestimate the
 441 oxygen concentration in this oxygen minimum zone and leads to a lack of local N_2O production.
 442

443 The relationship between N_2O concentration and OHC300 in the Tropical Ocean is derived from
 444 a linear regression for each of the three 20-years simulations (Figure 6). The resulting slopes

445 allow to identify three distinct tropical N₂O production pathways along time as a function of
 446 the oceanic heat uptake: from 0.3 μmolN m⁻² per ZJ for the most simplified PLF scenario
 447 climZCST, to 1 μmolN m⁻² per ZJ for climZVAR. The slope of the simulation with the higher level
 448 of realism in terms of interactivity (REF) appears a solution between the two previous extremes,
 449 as it increases its N₂O production by 0.8 μmolN m⁻² per ZJ. Each of these N₂O production
 450 pathways will translate into a different temporal evolution of the N₂O budget and hence future
 451 climate. This result stresses the importance of having an interactive PLF in order to neither
 452 overestimate nor underestimate the N₂O production projections due to a simplified
 453 representation of the PLF.
 454



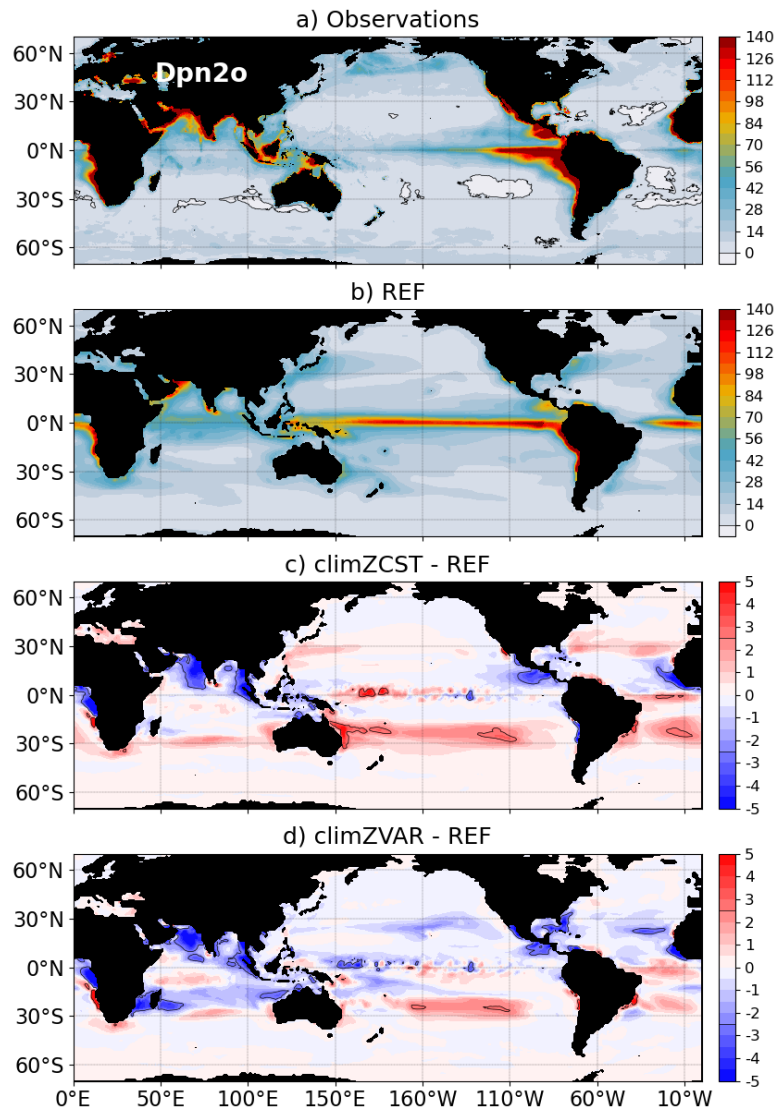
455 Figure 6: Annual N₂O inventory vertically integrated over the first 300 meters depth
 456 (μmolN/m²) as a function of the annual OHC300 (ZJ) and averaged over an extended tropical
 457 domain (35°S-35°N). All points reflect anomalies compared to year 1999.
 458

459
 460 **c) Impacts on oceanic N₂O emissions**
 461

462 By perturbing the OHC, the ocean dynamics and the N₂O production, the way PLF is modelled
 463 has non-negligible consequences on Dpn_{2o} and thus on N₂O emissions at the air-sea interface
 464 (Figure 7). Because the atmospheric partial pressure of N₂O is identical among simulations,
 465 differences in Dpn_{2o} are driven by changes in surface oceanic N₂O concentration normalized
 466 by those in N₂O solubility. Since solubility is mainly driven by temperature and because surface
 467 temperature anomalies are very weak (Figure S3, c and d), we do not expect solubility
 468 perturbations close to the surface. It results that spatial patterns of Dpn_{2o} anomalies (Figure
 469 7) reflect differences in surface oceanic N₂O concentration.
 470

471 Compared to a scenario considering a fully interactive PLF (REF), an incomplete representation
472 of the PLF underestimates D_{pn2o} in all oxygen minimum zones of the northern hemisphere,
473 which are strong emission zones (Figure 7, c and d). Large D_{pn2o} anomalies of -2.5 natm
474 encompasses northern parts of the oxygen minimum zones of the Indian, Pacific and Atlantic
475 oceans and anomalies reach up to -5 natm locally. Consequently, climZCST and climZVAR
476 underestimate N_2O fluxes by more than 12% in these oxygen minimum regions compared to
477 REF. This result highlights that the representation of the PLF can be an important source of
478 uncertainty in modelling N_2O fluxes. As a matter of fact, the oceanic contribution to the recent
479 global N_2O budget by Tian et al. (2020) is based on only five global ocean-biogeochemical
480 models (as still only few models simulate marine N_2O emissions). These models have different
481 configurations of the PLF which adds considerable uncertainty to simulated marine N_2O
482 emissions.

483
484 In subtropical gyres, the strong and direct effect of temperature (Figure S2, c and d) on in-depth
485 N_2O concentration (Figure 5, e and f) is in line with Yang et al. (2020) who demonstrate that the
486 seasonality of D_{pn2o} in that regions is driven by a solubility regime. Both climZCST and
487 climZVAR overestimate D_{pn2o} in subtropical gyres of the South Pacific and South Atlantic
488 (Figure 7, c and d). This leads to an overestimation of the regional N_2O fluxes by 24% compared
489 to a simulation having a complete and interactive PLF representation (REF).
490



491
 492 Figure 7: Mean sea-to-air D_{pn2o} (natm) computed from a) observations, b) REF over the 2009-
 493 2018 period, and its differences with c) climZCST and d) climZVAR compared to REF.

494
 495 **4. Discussion and conclusion**

496
 497 In this study we use the ocean component (including ocean physics, sea ice and marine
 498 biogeochemistry) of the global Earth system model CNRM-ESM2-1 which contributed to the
 499 last phase of the Coupled Model Intercomparison Project (CMIP6). Our ocean-biogeochemical
 500 model is one of the few currently able to represent an interactive phytoplankton-light feedback
 501 (PLF) by constraining the penetration of shortwave radiation into the ocean as a function of the
 502 CHL concentration produced by the biogeochemical model. Three simulations have been run
 503 at the horizontal resolution currently used for intercomparisons of Earth system models (1°).
 504 Analyses are based on differences between a control run with an interactive PLF (REF) and two
 505 experiments with an incomplete PLF (climZCST and climZVAR) using a prescribed CHL
 506 climatology to interact with the incoming solar radiation. Changing the approach to compute
 507 how CHL filters the light penetrating into the ocean highlights the consequences of using an
 508 interactive PLF.
 509

510 Our results demonstrate that the approach commonly used to account for the impact of the
511 phytoplankton on light penetration significantly interferes with upper ocean heat uptake (Figure
512 1), the associated dynamics (Figure 4) and stratification in the tropics (Figure 5, a-c). Our set of
513 forced ocean-biogeochemical simulations reveals that marine production of nitrous oxide
514 (N_2O) is sensitive to the representation of the PLF (Figure 5, d-f). The heat perturbations add to
515 the uncertainty of modelled oceanic N_2O production and result in three N_2O production
516 trajectories along time (Figure 6) that in turn trigger regional differences of D_{pN_2O} and sea-air
517 N_2O fluxes (Figure 7). Compared to an ocean model using a fully interactive PLF (REF), an
518 incomplete PLF results in an overestimation of N_2O fluxes by up to 24% in the South Pacific and
519 South Atlantic subtropical gyres, and a reduction by up to 12% in oxygen minimum zones of the
520 northern hemisphere. Our results based on a model at CMIP6 state-of-the-art emphasize an
521 overlooked important source of uncertainty in climate projections of marine N_2O production
522 and in current estimations of the marine nitrous oxide budget.

523
524 In subtropical gyres of the southern Hemisphere which are regions of low productivity, small
525 CHL changes have a strong and direct effect on temperature (Figure S2, c and d), transport
526 (Figure 4, b and c) and local stratification (Figure 5, b and c). These concomittant effects result
527 in a local decrease of N_2O concentrations in both experiments with a simplified PLF
528 representation (climZCST and climZVAR).

529
530 In forced ocean simulations, atmospheric forcings constrain surface temperature, salinity and
531 thus solubility. However, the N_2O concentration integrated over the upper 300 meters depth
532 of the water column (Figure 5, e-f) showed differences with the control run that follow those
533 of the in-depth temperature (Figure S2, c-d): in climZCST (climZVAR), a warmer (colder) tropical
534 ocean leads to a decreased (an increased) N_2O concentration. Because higher marine
535 greenhouse gas emissions will increase the temperature of the coupled atmosphere-ocean
536 system, adding an interactive atmospheric component is expected to amplify the PLF-induced
537 mean changes in marine N_2O concentration highlighted in this ocean-only numerical set (Park
538 et al., 2014; Asselot et al., 2022).

539
540 Our results also question the reliability of current modelled estimates of the area and volume
541 of oxygen minimum zones, as well as their trends in a future climate. The expansion rate of O_2 -
542 depleted waters still remains unclear and its controlling mechanisms are not yet fully
543 understood and represented in today's models. Observation based assessments suggested that
544 the ocean has already lost around 2% of the global marine oxygen since 1960 (Schmidtko et al.,
545 2017). The expansion of oxygen minimum zones is expected to result in an increase of the
546 volume of suboxic water and to have an impact on the production and decomposition of N_2O
547 (Freing et al., 2012). Our set of simulations highlights that an incomplete representation of the
548 PLF underestimates the expansion of oxygen-depleted waters over the 20 years of simulation
549 in comparison to REF. In climZCST and climZVAR the global volume (0-1000 m) of hypoxic water
550 with $[O_2]$ under 50 mmol m^{-3} is up to $2.3 \cdot 10^{14} \text{ m}^3$ lower in 2018 compared to that of the control
551 run REF. Thus an incomplete representation of the PLF might lead to an underestimation by 1.2
552 % of the modelled tropical volume of low-oxygenated waters after 20 years.

553
554 Recent regional studies demonstrated that the interactive PLF strongly affects upwelling
555 systems of the South Pacific and Atlantic oceans (Hernandez et al., 2017; Echevin et al., 2021).
556 Coastal upwellings are known to be sites of high N_2O production with an annual N_2O flux

557 amounting to approximately 20% of the global fluxes while these systems occupy less than 3%
558 of the ocean area (Yang et al., 2020). However, in the present study main modelled
559 perturbations are rather localized over oxygen minimum zones or subtropical gyres (Figure 5;
560 Figure 7). While the latter regional studies were performed at horizontal resolutions compatible
561 with the complex dynamics of coastal upwellings (from 10 km to about 28 km), the resolution
562 of climate models (~1-degree of horizontal resolution) does not allow to resolve these
563 dynamics. A step further would be to evaluate how the sensitivity of N₂O emission to the
564 representation of the PLF depends on the horizontal resolution by running simulations at higher
565 resolution with the same climate model. This would help to better determine how coastal
566 upwelling systems may impact the modelled N₂O inventory through different PLF
567 representations, as well as the associated modelled range of uncertainty.

568
569

570 **Code availability**

571 Sources for NEMO and PISCESv2 codes are available from <https://forge.nemo-ocean.eu/nemo>.

572

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578

579

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