

1 **Physical and biological processes driving seasonal variability of Nitrate**  
2 **budget and biological productivity in the Gabon-Congo upwelling system**

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33 Acronyms:

34 CTW: Coastally trapped waves

35 CoUS: Gabon-Congo Upwelling System

36 EKW: Equatorial Kelvin Waves

37 GG: Gulf of Guinea

38 MLD: Mixed Layer Depth

39 SST: Sea Surface Temperature

40 SSH: Sea Surface Height

41 SLA: Sea Level Anomaly

42 CHLa: Chlorophyll-a

43 EBUS: Eastern Boundary Upwelling System

44 TAUS: Tropical Angolan Upwelling System

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## 67 **Abstract**

68 The Gabon-Congo upwelling system, located in the southeastern Gulf of Guinea, is a highly  
69 productive marine ecosystem influenced by both local and remote physical forcing. This study  
70 investigates the seasonal variability of the nitrate budget and biological productivity in this region  
71 using a high-resolution (1/36°) coupled physical-biogeochemical simulation with the NEMO-PISCES  
72 model. The analysis highlights the relative contributions of physical and biological processes in  
73 modulating nitrate concentrations in both the mixed layer and the euphotic zone. Results reveal a  
74 semi-annual cycle of nitrate, with two upwelling periods (May–August and December) and two  
75 downwelling periods (January–April and October–November). These cycles are primarily driven by  
76 the passage of coastal trapped waves (CTWs) forced by equatorial Kelvin waves, inducing vertical  
77 thermocline displacements and regulating nitrate availability in the euphotic zone.

78 The nitrate budget analysis shows that the vertical diffusion linked to internal tide and local wind , and  
79 vertical advection linked to the CTWs, are the dominant process supplying nitrate to the mixed layer  
80 during the main upwelling season. However, near the Congo River mouth (5.5°S–6°S), the horizontal  
81 advection plays a key role, supplying significant amounts of nitrate through the river plume. In the  
82 lower euphotic layer, the vertical mixing contributes to the nitrate loss during the upwelling but  
83 becomes a source of nitrate during the downwelling periods. The seasonal cycle of the chlorophyll-a  
84 (CHLa) concentration follows that of nitrate, confirming that the primary production in this region is  
85 mainly driven by nitrate availability. The study also highlights the role of the Angola Current in  
86 transporting low-nitrate waters from the Equatorial Undercurrent, which influences the nitrate and  
87 CHLa balance in the Gabon-Congo upwelling system.

88 These findings provide new insights into the mechanisms governing nutrient dynamics and biological  
89 productivity in the Gabon-Congo upwelling system. Understanding these processes is crucial for  
90 assessing the impact of climate variability on the regional marine ecosystems and fisheries.

91 **Keywords:** Nitrate Budget, Gabon-Congo Upwelling System, NEMO-PISCES Model,  
92 Physical-Biogeochemical Interactions, Seasonal Variability, Coastal Trapped Waves

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## 101 **1 Introduction**

102 The Eastern Boundary Upwelling Systems (EBUS) are the most productive areas in the global ocean  
103 in terms of biological resources, hosting almost 20% of the world's fisheries (Chavez and Messie,  
104 2009, 2015), even though they only represent around 1% of the world's ocean surface (Freon et al.,  
105 2009). They are therefore an important economic support for the countries bordering these areas (Carr  
106 et al., 2002). EBUS are controlled by wind stress blowing parallel to the coast, generating an offshore  
107 Ekman transport leading to coastal upwelling of cold and nutrient-rich waters, which trigger primary  
108 production in the euphotic layer, with increased surface chlorophyll-a (CHL<sub>a</sub>) concentration visible on  
109 satellite images (e.g. Gutknecht et al., 2013). Besides their ecological richness, EBUS act as active  
110 interfaces for greenhouse gases. They are recognized as significant sources of  $N_2O$ , primarily due to  
111 the oxygen minimum zone (OMZ) that favors subsurface production (Gutknecht et al., 2013;  
112 Resplandy et al., 2024). Regarding  $CO_2$ , while cold surface waters enhance gas solubility, the vigorous  
113 upwelling of deep waters rich in Dissolved Inorganic Carbon (DIC) generally dominates this thermal  
114 effect, driving net  $CO_2$  outgassing near the coast (Resplandy et al., 2024).

115 Beyond these EBUS, recent studies (Bachèlery et al., 2016; Kopte et al., 2017; Awo et al., 2022) have  
116 shown that the variability of Sea Surface Temperature (SST, a key upwelling indicator) at the eastern  
117 boundary of the South Atlantic was not only impacted by local wind forcing, but also by remote  
118 forcing initiated by the equatorial dynamics. Indeed, the equatorial Kelvin waves (EKW) propagating  
119 along the equator and later poleward along the coast as coastal trapped waves (CTW) have been shown  
120 to lead to the establishment of seasonal upwelling systems.

121 This is the case for the Gabon-Congo and Angolan tropical upwelling systems, located in the  
122 south-east of the Gulf of Guinea (GG), which are highly productive marine ecosystems (Ostrowski et  
123 al., 2009). Fishing provides around 25% of the Angolan population's total animal protein intake and is  
124 essential for economic security (Hutchings et al., 2009; Sowman and Cardoso, 2010; FAO, 2022). The  
125 seasonal variability of SST along the Angolan coast has shown an evolution that was similar to that  
126 observed in the Congo (Bachèlery et al., 2015, 2016; Kopte et al., 2017; Awo et al., 2022; Brandt et al.,  
127 2023). It ~~is~~was characterized by a semi-annual pattern with an initial warming in February-April  
128 followed by a first upwelling-induced cooling in May-August. Then there ~~is~~was a second warming,  
129 less significant than the first, in September-November, followed by a second, less significant cooling  
130 in December-January. Following to Radenac et al. (2020) and Brandt et al. (2023), in the tropical  
131 Atlantic ocean, the thermocline and nitracline were often found at the same depth, which meant that an  
132 upward movement of the thermocline was associated with upward advection of nitrate, fueling  
133 biological productivity. Brandt et al. (2023) also pointed out that in the Angolan tropical upwelling  
134 system, the seasonal cycle of nitrate was in phase with that of CHL<sub>a</sub> derived from ocean color  
135 satellites (Fig. 1). Given that the wind stress along the coast was low for most of the year and out of

136 phase with the upwelling period, the upwelling was rather shown to be induced by the passage of  
137 waves trapped at the coast, which signature was visible on the seasonal cycle of the sea level anomaly  
138 (Bachèlery et al., 2016; Awo et al., 2022; Brandt et al., 2023).

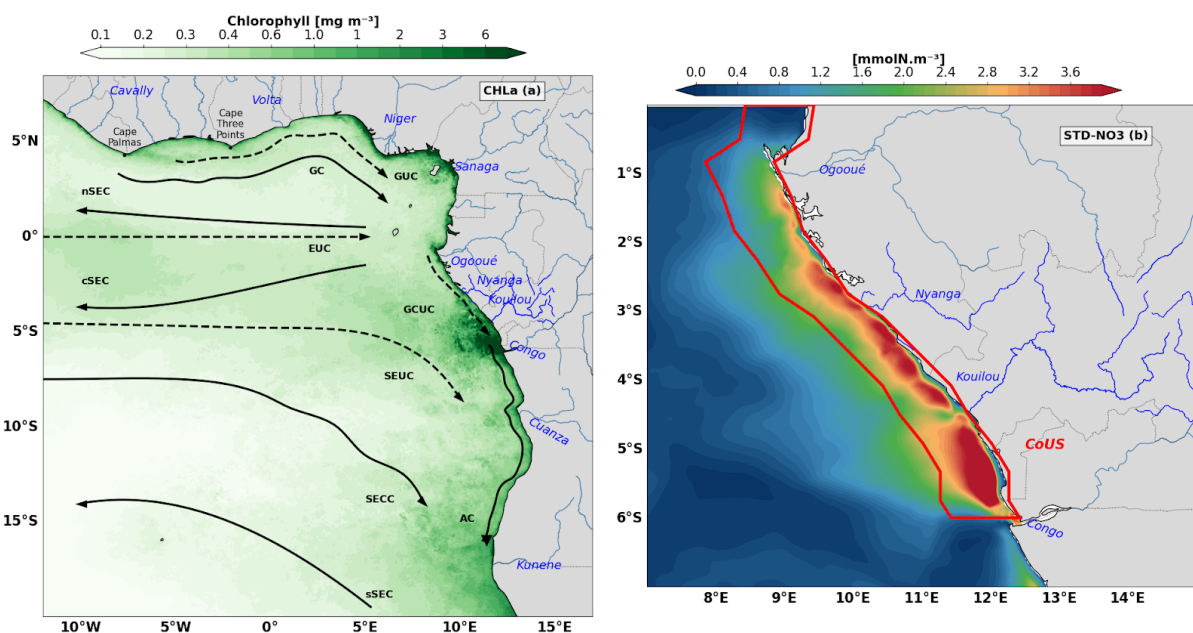
139 The cross-shore extension of the zone covered by upwelling ~~iswas~~ modulated by the regional ocean  
140 circulation (Fig. 1), dominated by the southward coastal Angola Current and Congo-Gabonese  
141 Undercurrent (Kopte et al., 2017; Bachèlery et al., 2016; Awo et al., 2022). Bachèlery et al. (2016),  
142 based on a coupled physical-biogeochemical model, showed that equatorial remote forcing ~~iswas~~  
143 dominant for the interannual variability of nutrients and primary production, whereas the local wind  
144 stress forcing ~~iswas~~ dominant for the sub-seasonal variability. Some studies also highlighted the  
145 important role played by turbulent mixing, locally enhanced in shallow waters near the coast (Körner  
146 et al., 2023, 2024; Tchipalanga et al., 2018a; Rouault, 2012), in the seasonal modulation of SST and  
147 nutrients in Angolan coastal waters.

148 The Gabon-Congo upwelling zone (from 0°N to 6°S) is poorly documented. In a recent study using a  
149 high resolution (1/36°) simulation of the NEMO model over the GG, Ngakala et al. (2025) assessed  
150 the seasonal mixed layer heat budget in the Congolese upwelling system. They found that the mixed  
151 layer heat budget in the Congolese coastal area was driven by two major processes: warming by heat  
152 fluxes, dominated all year long by the solar flux, and cooling by vertical mixing at the base of the  
153 mixed layer. whereas the total advection contribution is less important, it ~~playsplay~~ a secondary role in  
154 the mixed layer heat budget. However, below the mixed layer, vertical advection by upwelling CTWs  
155 was crucial to raise the thermocline high enough so that cool waters can penetrate in the mixed layer  
156 by vertical mixing. They also mentioned that the relative contribution of vertical advection and  
157 diffusion in the mixed layer heat budget was sensitive to the criterion used to define the mixed layer.

158 These results were in agreement with the conclusion of Körner (2023) in the northern Angolan  
159 upwelling south of the Congo River mouth. This latter study found that the net surface heat flux  
160 warmed the coastal water further, whereas turbulent mixing across the base of the mixed layer was an  
161 important cooling term. Also, Scannell and McPhaden (2018), using data from a PIRATA mooring  
162 located off the Congo River at [8°E; 6°S], found that the seasonal evolution of mixed layer properties  
163 had two main phases: a warm fresh phase (December-April) when solar heating was very efficient in  
164 warming SST in a thin mixed layer, and a cold-salty phase (May-September) driven by the  
165 intensification of southeasterly trades in response to the onset of the West African Monsoon and  
166 northward displacement of the ITCZ. They also pointed out the necessity to take into account  
167 precipitation influence in the mixed layer heat budget.

168 Little information has been available at the seasonal scale for biogeochemistry in the GG. In the  
169 equatorial upwelling system, the respective contributions of physical and biological processes on the

170 seasonality of nitrate and biological productivity, in the mixed layer and euphotic layer, have been  
 171 quantified by Radenac et al. (2020). Along the coast, most studies of biogeochemical dynamics have  
 172 been either limited to the section between 6°S and the Angola Benguela frontal zone (Brandt et al.,  
 173 2023), or have focused on the interannual variability of biogeochemical tracers (Bachelery et al.,  
 174 2016). The seasonal variability of biogeochemical tracers and biological productivity between 0°N and  
 175 6°S is likely influenced by three major processes: coastal upwelling, input of nutrients by the Congo  
 176 River discharge (which is the second largest river discharge in the world; Hopkins et al., 2013), and the  
 177 stratification linked to the Congo River freshwater. The aim of this paper is to investigate the  
 178 respective roles of physical and biological processes in the seasonal cycle of nitrate and CHLa  
 179 concentration, and the respective contributions of coastal upwelling and Congo River discharge to the  
 180 biological productivity in the Gabon-Congo upwelling system. The paper is organized as follows:  
 181 Section 2 describes the numerical model and datasets; Section 3 presents the model validation and the  
 182 nitrate budget analysis; Section 4 discusses the physical-biological interactions, and Section 5 provides  
 183 the conclusions.



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185 **Figure 1:** Regional ocean circulation and spatial distribution of biological and nutrient tracers.

186 (a) Annual mean surface Chlorophyll-a concentration ( CHLa,  $\text{mg m}^{-3}$ ). The map illustrates the spatial  
 187 distribution of biological productivity across the Gulf of Guinea and the South Atlantic African margin. Black  
 188 arrows and dashed lines indicate the major surface and subsurface currents: northern, central and southern  
 189 branches of the South Equatorial Current (nSEC, cSEC and sSEC , respectively), Equatorial Undercurrent  
 190 (EUC), Guinea Current (GC), Guinea Undercurrent (GUC), Gabon-Congo Undercurrent (GCUC), South  
 191 Equatorial Undercurrent (SEUC), South Equatorial Counter Current (SECC), and Angola Current (AC). (b)  
 192 Standard deviation of Nitrate concentration ( STD-NO3,  $\text{mmolN m}^{-3}$ ). The color scale represents the  
 193 variability of nitrates in the upper ocean. The red polygon delimits the coastal domain defined as the  
 194 Gabon-Congo Upwelling System (CoUS), extending from the Congo River mouth ( $\sim 6^\circ\text{S}$ ) to the Equator ( $\sim 0^\circ\text{S}$ ),

195 which serves as the primary study area for the nutrient budget analysis. Blue labels highlight the discharge points  
196 of the Ogooué, Nyanga, Kouilou, and Congo rivers.

## 197 **2 Data and methods**

### 198 **2.1 Numerical model**

199 To understand the dynamics in the Gabon-Congo upwelling system, we have used the NEMO  
200 (Nucleus for European Modelling of the Ocean) ocean general circulation model based on the  
201 primitive equations discretized on an Arakawa-C grid (Madec et al., 2024). The vertical mixing is  
202 computed from a turbulent closure scheme using the GLS (Generic Length Scale) formulation.

203 In this work, the NEMO model was coupled with PISCES (Pelagic Interactions Scheme for  
204 Carbon and Ecosystem Studies), a biogeochemical model developed by Aumont et al. (1998) and  
205 subsequently improved. Here, the version used is PISCES-2 (Aumont et al., 2015). This model has  
206 three main compartments: the first represents nutrients, including nitrogen compounds (nitrate and  
207 ammonium), iron, phosphate and silicates; the second represents phytoplankton and includes two  
208 classes, nano-phytoplankton and diatoms; the third compartment represents zooplankton, made up of  
209 two classes, microzooplankton and meso-zooplankton. We used the PISCES (cell quotas) model with  
210 constant Redfield ratios (Aumont and Bopp, 2006; Aumont et al., 2015).

211 A regional configuration of the GG (11°S - 6°N; 10°W - 14°E) with an horizontal resolution  
212 of 1/36° and 50 vertical levels is used. The atmospheric forcing is derived from the JRA-55 reanalysis  
213 of the Japanese meteorological agency (Kobayashi et al. 2015), except for the wind forcing which is  
214 based on daily ASCAT (Advanced SCATterometer) satellite data at 1/4° spatial resolution. Lateral  
215 boundaries conditions are from Mercator GLORYS12V1 reanalysis data at 1/12° spatial resolution for  
216 physics and NEMO-PISCES reanalysis at 1/4° of Radenac et al. (2020) for biogeochemistry.  
217 Continental freshwater inputs for this configuration are derived from the ISBA-CTRIP model, and in  
218 situ data from the HYBAM network for the Congo River. The NEMO configuration, ran over the  
219 period 2007-2017 (after a two-year spin-up), was validated by Ngakala et al. (2025) in our region of  
220 study. This simulation has also been validated and used in the Northern Gulf of Guinea for the coastal  
221 upwelling in summer and its interaction with mesoscale dynamics (Thiam et al., 2024). The reference  
222 simulation of the coupled biogeochemical physical model (NEMO-PISCES) was produced over the  
223 period 2007-2011, with a spin-up of 4 years for the biogeochemical part (2007-2010). We analysed  
224 monthly and daily outputs for the year 2011, which is characterised by neutral conditions regarding the  
225 Atlantic Niño and Benguela Niño interannual variability (Brandt et al., 2023).

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## 228 2.2 Satellite and in-situ data

229 Several observational products were used to assess the model's ability to reproduce the physical and  
230 biogeochemical characteristics of the area for the year 2011. We used the MUR product (Multi-scale  
231 Ultra-high Resolution; Chin et al., 2017) with 1/4° spatial resolution and daily temporal resolution to  
232 assess the regional distribution and the seasonal cycle of SST. The vertical temperature distribution  
233 was assessed using the World Ocean Atlas (WOA; Locarnini et al., 2018; Zweng et al., 2019)  
234 climatology. The CHLa data used came from the Globcolour product distributed by Copernicus Marine  
235 Environment Monitoring Service (<http://marine.copernicus.eu/>), which combines data from four ocean  
236 color satellites, with very high spatial resolution (1 km) and daily temporal resolution.

237 The nutrient fields were assessed using the CSIRO Atlas of Regional Seas climatology  
238 (Ridgway and Dunn, 2002) which merges several in situ databases (Argo buoys, WOD2005, WOCE3,  
239 Global Hydrographic Program, CTD and CMAR4 hydrology archives, NIWA5 hydrographic data, and  
240 CRC6 hydrographic data). It provides physical variables (Temperature, Salinity) and biogeochemical  
241 variables ( $NO_3$ ,  $PO_4$ ,  $O_2$ , Si) both at the surface and at depth with a horizontal resolution of 1/2 °, 79  
242 vertical levels from the surface to 5500 m depth, with a step of 5 m near the surface then increasing  
243 with depth, and a daily temporal resolution. This product was built from 2009 and contains data from  
244 1940 until 2011 which was the date when the last revision of the product was made. Near surface  
245 currents from the Ocean Surface Current Analysis Real-time (OSCAR, Johnson et al. 2007) dataset are  
246 based on satellite and in situ measurements of sea surface height surface vector wind and SST. They  
247 are derived from quasi-linear and steady flow momentum equations thus combine geostrophic, Ekman  
248 and Stommel shear dynamics. OSCAR product is available on a 1/3°×1/3° grid with a 5-day temporal  
249 resolution for year 2011, and we use it to validate the near surface currents (first 30 meters) of the  
250 model outputs. Sea Level Anomaly was computed from the salto/duacs gridded product of Absolute  
251 Dynamic Topography for 2011. This product is based on sea surface height measurement of  
252 multimission altimeters since 1992, optimally interpolated onto 0.25° x 0.25° longitude/latitude grid  
253 (Ducet et al., 2000).

## 254 2.3 Methods

255 The variability of nutrients and in particular nitrate is driven by several physical and biogeochemical  
256 processes taken into account in our model. As in Radenac et al (2020), the nitrate budget integrated  
257 over the mixed layer depth is represented by the following equation:

$$258 \frac{\partial \langle NO_3 \rangle}{\partial t} = - \langle u \frac{\partial NO_3}{\partial x} \rangle - \langle v \frac{\partial NO_3}{\partial y} \rangle - \langle w \frac{\partial NO_3}{\partial z} \rangle + \frac{1}{h} \left( K_z \frac{\partial NO_3}{\partial z} \right)_{z=-h} - \frac{1}{h} \frac{\partial h}{\partial t} \left( \langle NO_3 \rangle - NO_{3_{z=-h}} \right)$$

259 +  $SMS(NO_3)$  (1)

260 In Equation (1), the term on the left represents the total nitrate tendency, where the brackets  $\langle \dots \rangle$   
 261 denote the vertical average within the mixed layer of depth  $h$ . This depth  $h$  is defined as the level  
 262 where the potential density exceeds the reference density at 3 meters by approximately  $0.06 \text{ kg/m}^3$   
 263 (Aroucha et al., 2025). On the right side of the equation, the first three terms represent the zonal,  
 264 meridional, and vertical advectons of nitrate, respectively, with  $u, v$  and  $w$  being the components of the  
 265 velocity field. The fourth term represents the vertical diffusion (mixing) at the base of the mixed layer  
 266 ( $z=-h$ ), where  $K_z$  is the vertical diffusion coefficient that varies in space and time. The fifth term  
 267 corresponds to the entrainment term, which represents the flux of nitrate into the mixed layer during its  
 268 deepening. However, it is not explicitly solved in our budget analysis. Following Radenac et al. (2020)  
 269 for the tropical Atlantic using a similar NEMO-PISCES configuration, this term is negligible  
 270 compared to other terms in the budget. Finally, the SMS (Source Minus Sink) term represents the  
 271 contribution of biological processes to the spatial and temporal variability of  $\text{NO}_3$  concentrations, as  
 272 detailed in the following expression:

$$273 \text{SMS}(\text{NO}_3) = \text{Nitri}f - \mu_{\text{NO}_3}^P * P - \mu_{\text{NO}_3}^D * D - R_{\text{NH}_4} * \lambda_{\text{NH}_4} * \Delta(\text{O}_2) * \text{NH}_4 - R_{\text{NO}_3} * \text{Denit} \quad (2)$$

274 where *Nitri*f corresponds to nitrification, which is the conversion of ammonium into nitrate by  
 275 bacterial activity. It is parameterized by:

$$276 \text{Nitri}f = \lambda_{\text{NH}_4} - \frac{\text{NH}_4}{1 + \langle \text{PAR} \rangle} (1 - \Delta(\text{O}_2)) \quad (3)$$

277 where  $\text{NH}_4$  is the ammonium concentration,  $\langle \text{PAR} \rangle$  is the average fraction of solar radiation available  
 278 for photosynthesis,  $\lambda_{\text{NH}_4}$  is the nitrification rate and  $\Delta(\text{O}_2)$  is the oxygen variation in the mixed layer,  
 279 which provides information on the oxic and anoxic conditions of the water column: The second and  
 280 third terms on the right of equation (2) are the growth of nanophytoplankton and diatoms, where  $\mu_{\text{NO}_3}^P$   
 281 and  $\mu_{\text{NO}_3}^D$  are their growth rates,  $P$  and  $D$  are their concentrations respectively.  $R_{\text{NH}_4}$  and  $R_{\text{NO}_3}$  are the  
 282 stoichiometric  $N/C$  ratios of ammonification and nitrification respectively.. *Denit* represents  
 283 denitrification which occurs when the water becomes anoxic, and so nitrate (instead of oxygen) is  
 284 consumed by remineralization of organic matter. A detailed description of the terms of these equations  
 285 is given by Aumont et al (2015). We used the parameter PISCES values modified for the Tropical  
 286 Atlantic ocean from Radenac et al. (2020). The balance terms in equation (1) have been calculated  
 287 online for 2011. As the lateral diffusion term is generally negligible compared with the others, it will  
 288 not be discussed further.

289 Since the advection in (1) depends on both nitrate gradients and velocities, we investigate which  
 290 component primarily controls its contribution. First, we analyze the seasonal evolution of gradient and

291 velocity following Awo et al. (2022). Second, we evaluate the individual contributions of seasonal  
 292 variations in velocity and gradient, as well as their combined effect, following Topé et al. (2023),  
 293 according to equation (4).

$$294 \left( V_i \cdot \nabla_i (NO_3) \right)' = V_i' \cdot \overline{\nabla_i (NO_3)} + \overline{V_i} \cdot \nabla_i (NO_3)' + V_i' \cdot \nabla_i (NO_3)' \quad (4)$$

295 The total seasonal variation of the advection term is thus decomposed into three distinct contributions:

296  $V_i' \cdot \overline{\nabla_i (NO_3)}$  (Current variability), this term quantifies the impact of current velocity anomalies acting  
 297 upon a mean (steady-state) nitrate distribution. It isolates the effect of current acceleration or  
 298 intensification (such as the SEUC or the Angola Current) on nutrient transport.  $\overline{V_i} \cdot \nabla_i (NO_3)'$  (Gradient  
 299 variability), this term represents the impact of seasonal changes in the nitrate concentration gradient  
 300 under a mean circulation. It highlights the influence of seasonal water mass enrichment, particularly  
 301 via the Congo River plume.  $V_i' \cdot \nabla_i (NO_3)'$  (Non-linear term), this term accounts for the simultaneous  
 302 interaction between current fluctuations and gradient fluctuations. To determine which of these  
 303 mechanisms predominantly governs the nitrate budget, Pearson correlation coefficients were  
 304 calculated between the total advective anomaly and each decomposed component. This statistical  
 305 approach serves a critical physical objective: it allows us to disentangle whether the seasonal nitrate  
 306 supply is driven primarily by the kinematic modulation of the flow (circulation-driven) or by the  
 307 pulsing of the nutrient source (supply-driven). A high correlation with the current term would identify  
 308 regional circulation such as the SEUC or Angola Current as the primary pump, whereas a dominant  
 309 correlation with the gradient term would pinpoint the massive periodic enrichment, particularly from  
 310 the Congo River plume, as the main trigger of nitrate variability. All reported correlations are  
 311 statistically significant at a 95% confidence level ( $p < 0.05$ ). By establishing this statistical hierarchy,  
 312 we can physically characterize the system as being either transport-limited or supply-limited,  
 313 providing a rigorous diagnostic of the processes regulating primary productivity in the Gabon-Congo  
 314 upwelling. The Primary production (NPP) was calculated from the phytoplankton evolution equation  
 315 (Aumont et al 2015):

$$316 \quad NPP = (1 - \delta^P) \mu^P * P \quad (5)$$

317 In this equation, P is the phytoplankton biomass (diatoms),  $\delta^P$  represents the exudation of the  
 318 phytoplankton (diatoms).  $\mu^P$  is the specific growth rate of the phytoplankton taking into account  
 319 nutrient and light availability. Note that this equation applies to each phytoplankton species (diatoms  
 320 or nanophytoplankton), and total NPP is the sum of NPP from both diatoms and nanophytoplankton.  
 321  $\mu^P$  is the specific growth rate of the phytoplankton taking into account nutrient and light availability.

322 NPP, which represents the organic matter synthesized by phytoplankton after accounting for  
323 autotrophic respiration, is calculated online by the coupled NEMO-PISCES model. Within the model  
324 framework, NPP is partitioned into New Production (NP), fueled by external nutrient inputs (primarily  
325 nitrate) through advection and diffusion, and Regenerated Production (RP), sustained by nutrients  
326 recycled within the euphotic zone (primarily ammonium). Both NP and RP components are computed  
327 online, providing a detailed breakdown of the trophic status and nutrient utilization efficiency in the  
328 Gabon-Congo upwelling system.

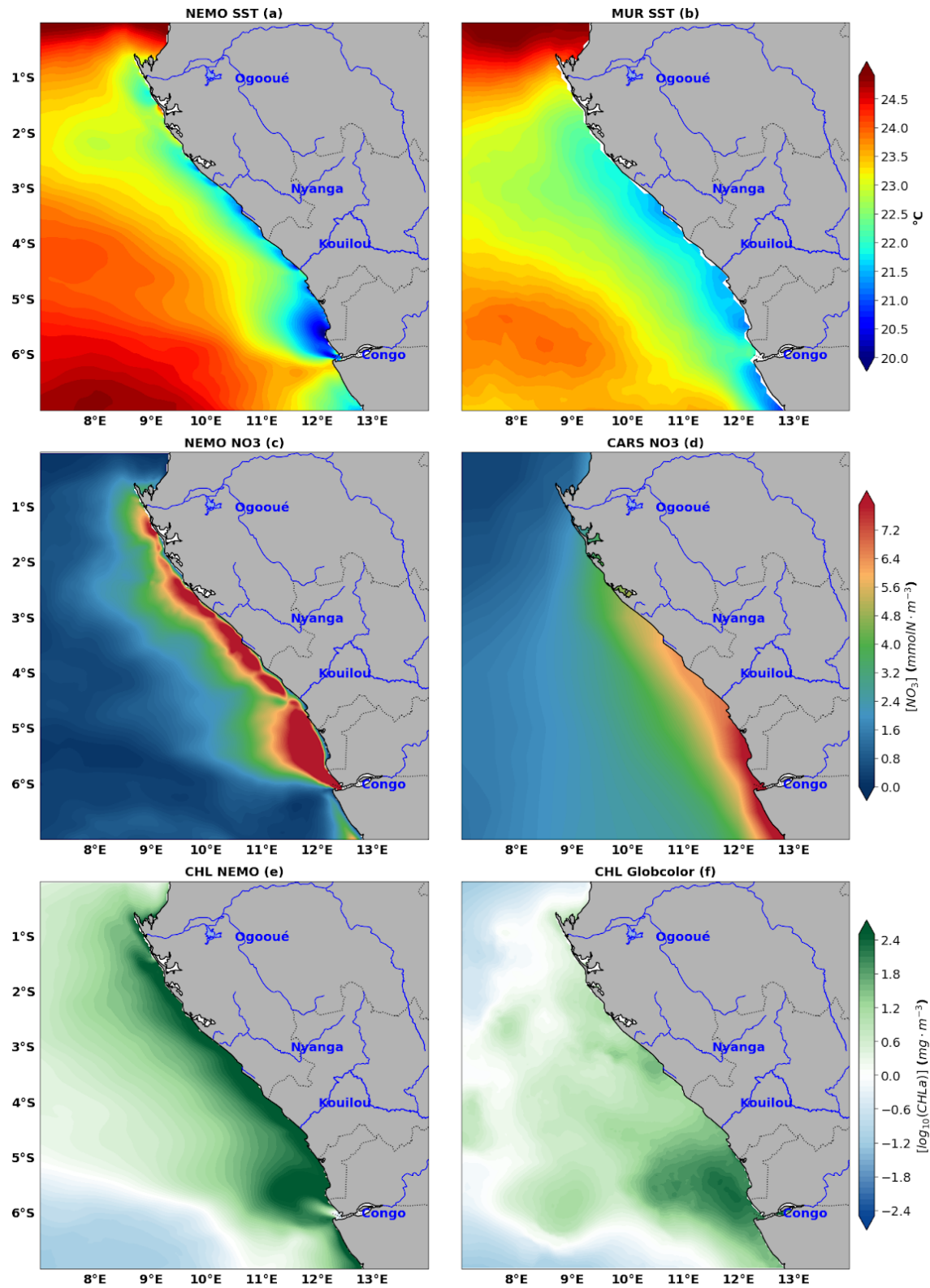
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## 330 **3 RESULTS**

### 331 **3.1 Model/data comparison**

#### 332 **3.1.1 Spatial variations during the upwelling period**

333 The assessment of our model simulation has been done using several observation products of physical  
334 variables, including Sea Surface Temperature (SST), Sea Surface Height (SSH), and ocean currents,  
335 as well as biogeochemical tracers such as nitrate ( $\text{NO}_3$ ) and CHLa, based on both satellite and in situ  
336 data. Fig.2 shows the regional distribution from observations and model outputs for both SST  
337 (Fig.2a-b), nitrate concentration (Fig.2c-d) and CHLa concentration (Fig.2e-f), averaged for austral  
338 winter (June, July and August) which is the main Gabon-Congo upwelling period (Ngakala et al.,  
339 2025). As can be seen, the upwelling feature is well captured by the model with cooling of surface  
340 water at the coast below  $23^\circ\text{C}$  in the model and  $22^\circ\text{C}$  in the MUR product (Fig. 2a,b). This cooling  
341 feature is consistent with high nitrate (Fig. 2c,d) and CHLa (Fig. 2e,f) concentrations in both models  
342 and observation, particularly north of the Congo estuary ( $6^\circ\text{S}$ ) and nearby Kouilou River mouth (Fig.  
343 2e) at  $4.47^\circ\text{S}$ . These cool and enriched nutrient coastal waters are spread offshore displaying a  
344 cross-shore gradient, with a greater extension in the observation than the model. The highest nitrate  
345 concentration in the coastal waters is greater than  $10 \text{ mmolN.m}^{-3}$  in the model ( $8 \text{ mmolN.m}^{-3}$  in the  
346 observation) located mainly in the Congo River plume area, inducing enhancement of PP resulting in a  
347 strong CHLa signature.



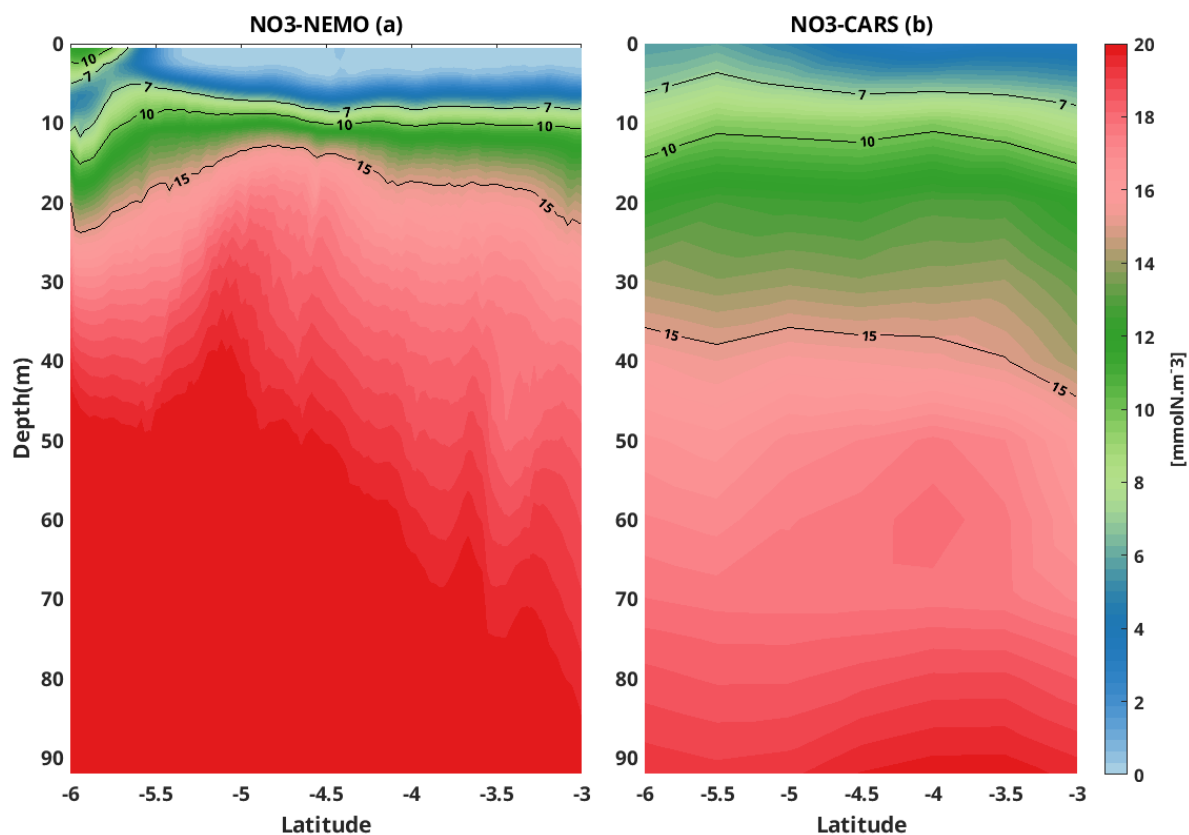
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349 **Figure 2:** Comparison between model (left hand side) and observations (right hand side) with regional  
 350 distribution of sea surface temperature (a, b), nitrate concentration (c, d) and CHLa concentration (e, f)  
 351 averaged for austral winter (June, July, August)

352 The offshore area (7°E-10°E) is the oligotrophic zone characterized by relatively warm waters (24.5°C  
353 in the model and 23.5°C in the observation), depleted in nitrate and less productive in CHLa  
354 concentration. In this offshore area nitrate concentrations are lower than 1.6 mmolN.m<sup>-3</sup> in the  
355 observation and 0.8 mmolN.m<sup>-3</sup> in the model.

356 Although the model captures relatively well the regional distribution of the 3 variables, we can see  
357 some differences. For instance, the model is warmer than observations by about 1°C and shows  
358 stronger nitrate concentration (by about 2 mmolN.m<sup>-3</sup>) and CHLa concentration (6-10 mg.m<sup>-3</sup>) at the  
359 coast. In the offshore area, the model seems to be less enriched in nitrate concentration than the  
360 observation by about 0.8 mmolN.m<sup>-3</sup>.

361 High variability of nitrate concentration is found in the coastal Gabon-Congo area (Fig.1b) and in the  
362 Congo river plume zone as we can see in model annual standard deviation distribution of NO<sub>3</sub>.  
363 Therefore the red box (0°S-6°S, 1° width coastal band) in Fig.1b is used to analyze the vertical nitrate  
364 profile to assess the model's ability to capture its vertical distribution. This area corresponds to our  
365 studied area in the Gabon-Congo coastal upwelling zone.

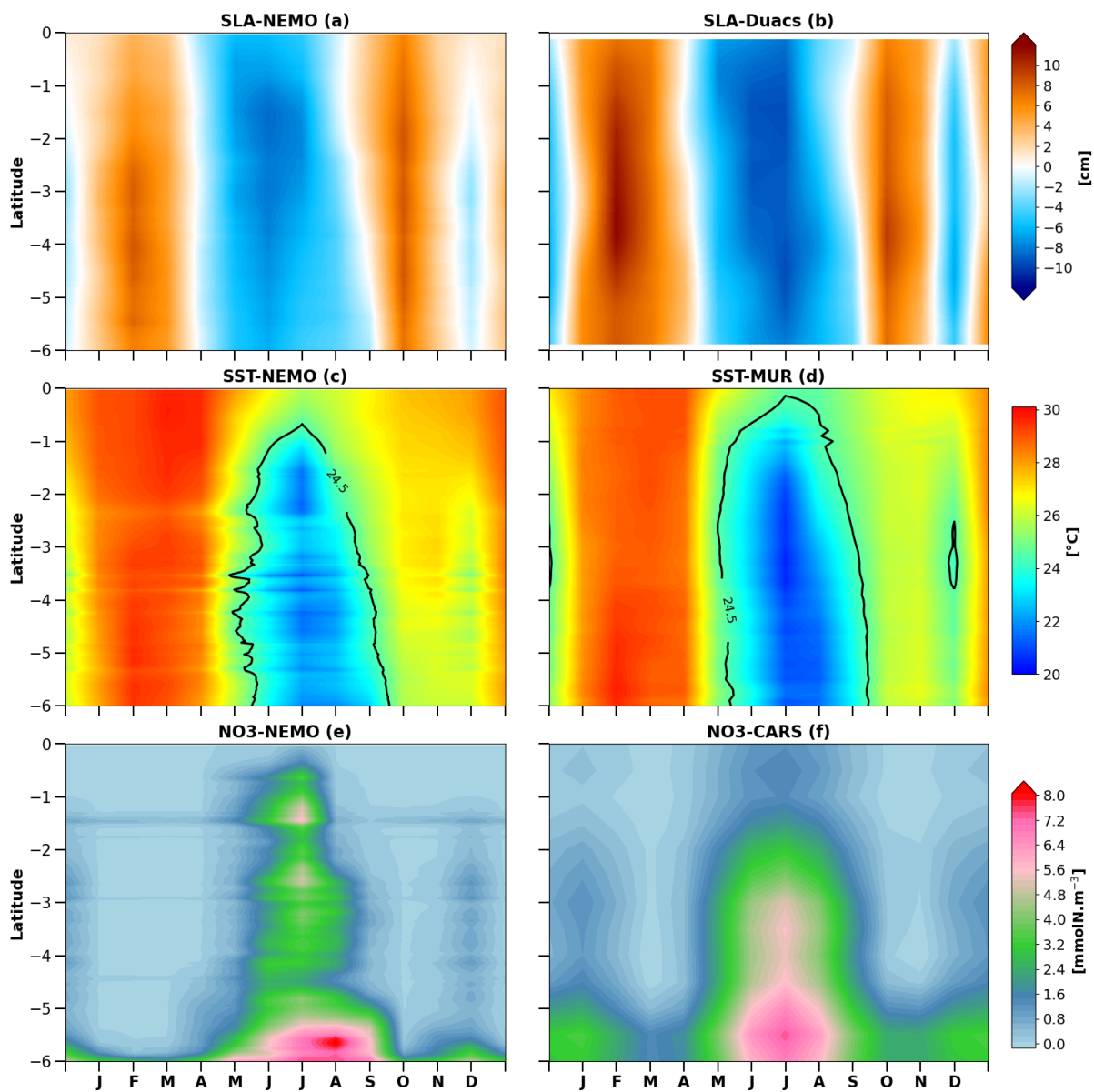


366  
367 **Figure 3:** Comparison between model (a) and observation (b) using vertical distribution of nitrate concentration  
368 in the first 90 m, in the coastal box (3°S-6°S and 1° width band to the coast) in the main upwelling season (June,  
369 July and August). black represents nitrate concentration isolines.

370 Very close to the surface, water masses are nutrient depleted for both model and observation (Fig.3),  
371 likely due to photosynthesis activity of phytoplankton that consumes nitrate in presence of light,

372 increasing its biomass thus CHLa concentrations. However this depletion is more pronounced in the  
 373 model than in the observation. In the subsurface, the high nitrate concentration is due to the  
 374 remineralization of organic matter by bacteria and coastal upwelling of deeper enriched nitrate waters,  
 375 with the model showing higher concentrations than observed. Although nitrate isolines are shallower  
 376 in the model than in observations below about 15 m depth, some nitrate isolines are relatively well  
 377 captured by the model, for instance isolines 7 and 10  $\text{mmolN.m}^{-3}$ .

### 378 3.1.2 Seasonal cycle of SST, nitrate, SLA and current in the Gabon-Congo coastal area



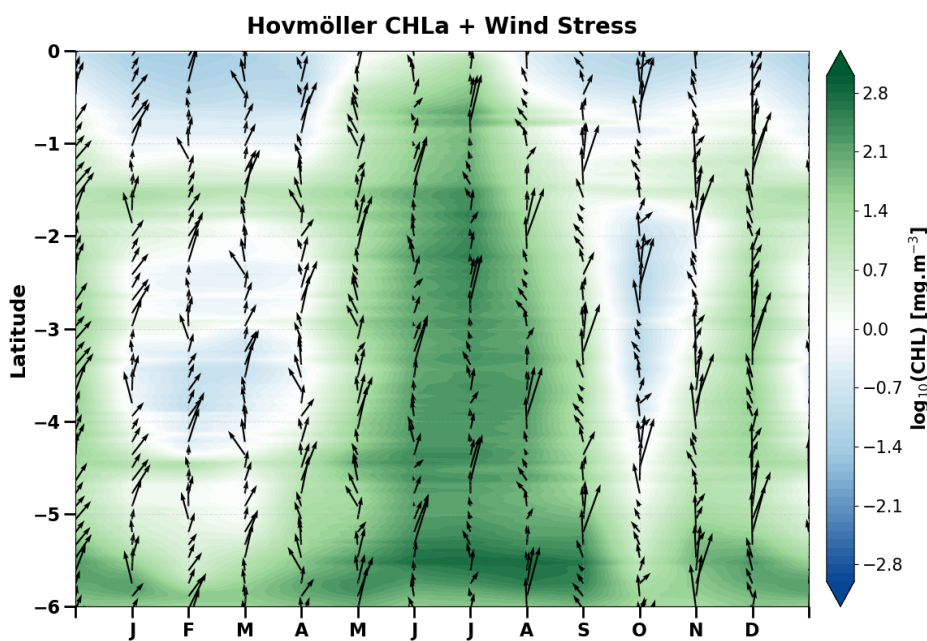
379  
 380 **Figure 4:** Comparison between modeled (left) and observed (right) seasonal cycles of Sea Level Anomaly (a, b),  
 381 SST(c, d) and nitrate concentration (e, f) averaged in the coastal box ( $6^{\circ}\text{S}$ - $0^{\circ}\text{S}$ ,  $1^{\circ}$  width).

382 Now we use the coastal box defined in Fig. 1b to evaluate the seasonal cycle of nitrate. The nitrate  
 383 seasonal variability is characterized by a semi-annual cycle with two maxima and two minima in the

384 model and the observations. The main maximum occurs from May to September when SST reaches its  
385 minimum of 20°C in both model and observations (Fig.4c, Fig.4d) and the secondary maximum occurs  
386 in December when SST reaches a secondary minimum of 25.5°C in the model and 24.5°C in  
387 observation. We have a warmer SST reaching 30°C from January to April and 26°C from October to  
388 November in both the model and the observations. This semi-annual SST cycle is likely due to CTWs  
389 propagation since it is consistent with the SLA seasonal cycle (minimum SST corresponds to negative  
390 SLA and maximum SST corresponds to positive SLA) as mentioned earlier by Ngakala et al. (2025) in  
391 the same area. Indeed, the propagation of CTWs induce vertical migration of the thermocline resulting  
392 thereby in cooling or warming at the surface. At the seasonal scale, the propagation of upwelling  
393 CTWs from May to September and in November-December uplifts thermocline, supplying cold waters  
394 to the surface and reducing Sea Surface Height (SSH) by steric effect. As downwelling CTWs  
395 propagate from January to April and in September-October, they deepen thermocline, warming the  
396 surface and increasing SLA. The cold waters upwelled by CTWs (May-September) are highly  
397 enriched in nitrate, whereas warm surface waters induced by downwelling CTWs (January-April and  
398 September-October) are nitrate depleted. The seasonal variability of SLA due to CTWs (Fig.4a,  
399 Fig.4b) is consistent with the seasonal variability of SST (Fig.4c, Fig.4d) and of nitrate concentration  
400 (Fig.4e, Fig.4f) in both the model and observations. The highest nitrate concentration is around 10  
401  $\text{mmol.m}^{-3}$  near the Congo River mouth (6°S) and decreasing northward, however the observations  
402 seem to be richer in nitrate than the model. In December during the secondary cooling, nitrate  
403 concentration in the model is greater by about 1.2  $\text{mmol.m}^{-3}$  than observed along the coast. In the  
404 warming period (January-April and October-November), this coastal area seems to be nitrate depleted.  
405 Despite the model capturing the SLA signature, the observed seasonal cycle of SLA remains more  
406 intense than in the simulation. This feature is driven by the combined effect of remotely forced  
407 Equatorial Kelvin Waves (EKW) and poleward-propagating CTWs (Bachèlery et al., 2016; Kopte et  
408 al., 2017; Awo et al., 2023; Brandt et al., 2023). During cooling periods, upwelling CTWs decrease the  
409 SLA and uplift the thermocline. Following Radenac et al. (2020), the thermocline depth in this region  
410 acts as a reliable proxy for the nitracline; its upward migration significantly enhances nitrate supply to  
411 the surface, fueling biological productivity. Conversely, the downwelling waves observed in the  
412 warming periods increase the SLA and deepen the nitracline, leading to the nutrient-depleted  
413 conditions described previously.

414 High nitrate concentrations support biological production, therefore correspond to high CHL<sub>a</sub> signals  
415 at the surface (Fig.5). On the contrary, during the warming period, the downwelling CTWs  
416 propagating along the coast increase SLA, deepen the thermocline (Ngakala et al. (2025). This also  
417 deepens the nitracline and consequently deplete the nitrate concentration at the ocean surface, thus the  
418 low CHL<sub>a</sub> signal (Fig.5).

419 The variability of simulated near-surface currents between 0 to 15 m depth (Fig.6) was compared to  
 420 the OSCAR product. Here, we make a latitudinal section at 4°S and look at the seasonal cycle of  
 421 meridional currents (Fig.6a and 6b) from 7°E to the coast for both the model (Fig.6a) and observations  
 422 (Fig.6b). We do not restrict to the Gabon-Congo box as we have done for other variables, because the  
 423 OSCAR product is not well resolved at the vicinity of the coast. So we can see that the model  
 424 reasonably represents the seasonal variability of meridional currents with northward velocities in  
 425 April, June-September and November-December with the magnitude of around 0.1 m.s<sup>-1</sup>. In the  
 426 observations, this structure is more or less similar, but we can see some differences: southward  
 427 velocities between 8.5°E and 10.2°E in July, and also between 7°E and 9°E during August-September  
 428 and January, are not found in the model.



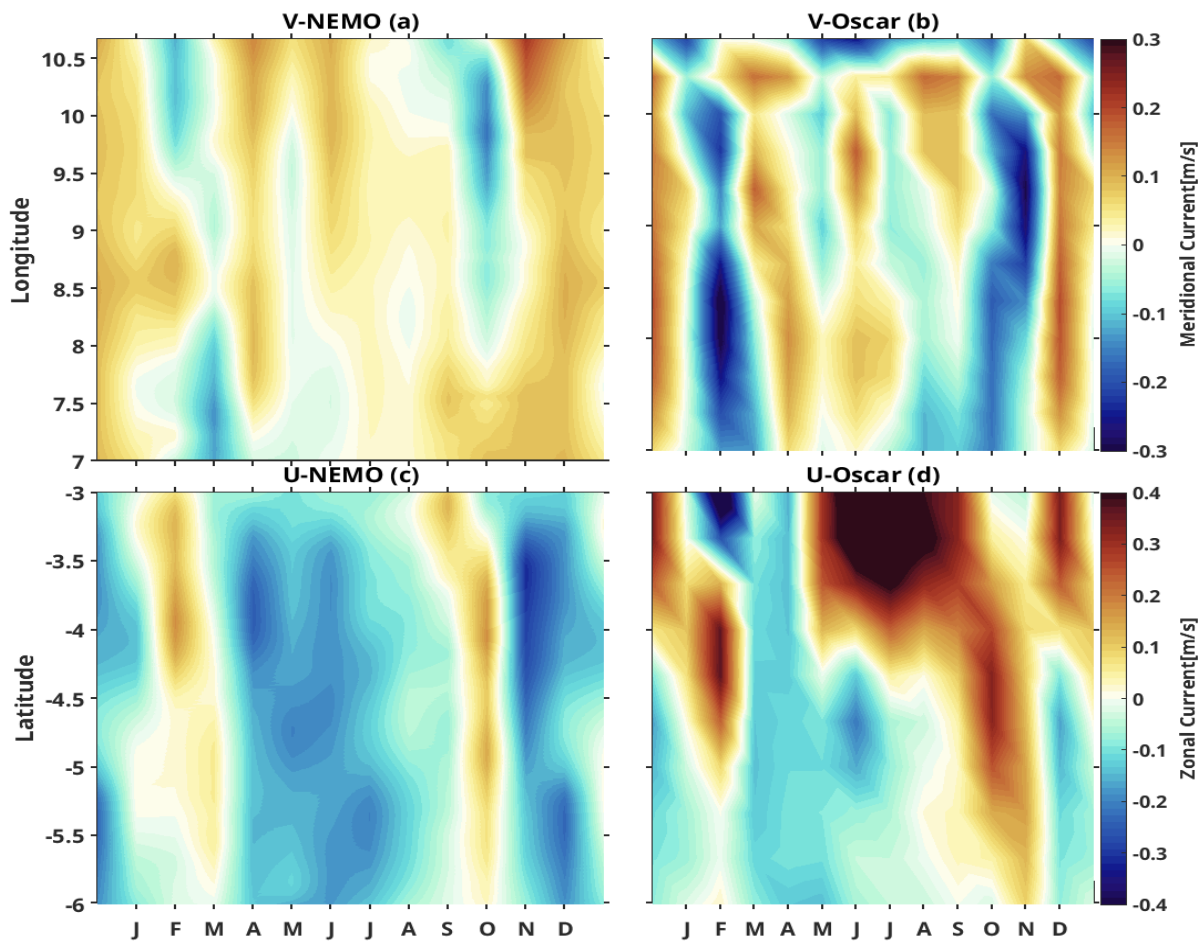
429  
 430 **Figure 5:** Seasonal cycle of CHLa concentration (in background) and wind stress (black arrow) along the  
 431 Gabon-Congo coastal box (6°S-0°S, 1° width) area in the model.

432 Nevertheless, we can see in both products southward currents in February-March and October with a  
 433 strong magnitude of 0.25 m.s<sup>-1</sup> in the observations though only 0.15 m.s<sup>-1</sup> in the model. This seasonal  
 434 structure is consistent with the seasonal cycle of meridional currents off Angola, further south, and the  
 435 southward flow in February-March and October seems to be the Angola current (Kopte et al 2017). To  
 436 assess the zonal current (Fig.6c and 6d), we make a longitudinal section at 10°E and we look at the  
 437 seasonal cycle of zonal current between 3°S and 7°S. The modeled zonal structure with westward  
 438 velocities from April to August and November – December has a magnitude of about 0.1 m.s<sup>-1</sup> along  
 439 the section (Fig.6c), in agreement with the observations (Fig.6d), which also show westward velocities  
 440 from April to August. However there are some differences with the model from March to August  
 441 between 3°S and 4.5°S where we can observe very strong (more than 0.5 m.s<sup>-1</sup>) eastward flow. In  
 442 contrast to the model, the flow during November is eastward in the observation. The noticeable

443 similitude is the eastward flow in January- February and October with a magnitude of  $0.15 \text{ m}\cdot\text{s}^{-1}$  which  
 444 seems to be the signature of the South Equatorial UnderCurrent (SEUC). This eastward current is  
 445 deeper further offshore (100 m depth) west of  $0^\circ\text{E}$  (Bourles et al., 2004) and rising near the surface  
 446 near the coast (Nubi et al., 2016; Assene et al., 2022).

### 447 3.2 Nitrate budget in the mixed layer

448 Generally, the seasonal variations in CHLa are thought to be primarily related to seasonal variations of  
 449 the nitrate input in the equatorial Atlantic ocean (Loukos and Mémerly., 1999; Radenac et al, 2020) and  
 450 in the tropical Angolan upwelling (Brandt et al., 2023). This is probably the case also in the  
 451 Gabon-Congo coastal area, where the seasonal cycles of nitrate (Fig.7a) and CHLa (Fig.5) in our  
 452 model are very consistent. Corresponding to the semi-annual variability of nitrate, the seasonal change  
 453 rate of its concentration (Fig. 8b) displays a four-phase cycle: a first increasing phase between March  
 454 and August with a highest amplitude ( $0.3 \text{ mmol}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ ) in July, followed by a decreasing phase in  
 455 ~~September~~ September–November with a highest amplitude in October ( $0.01 \text{ mmol}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$  north of  $5^\circ\text{S}$   
 456 and about  $-0.13$  to  $-0.3 \text{ mmol}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$  between  $5^\circ\text{S}$  and  $6^\circ\text{S}$  all years long).



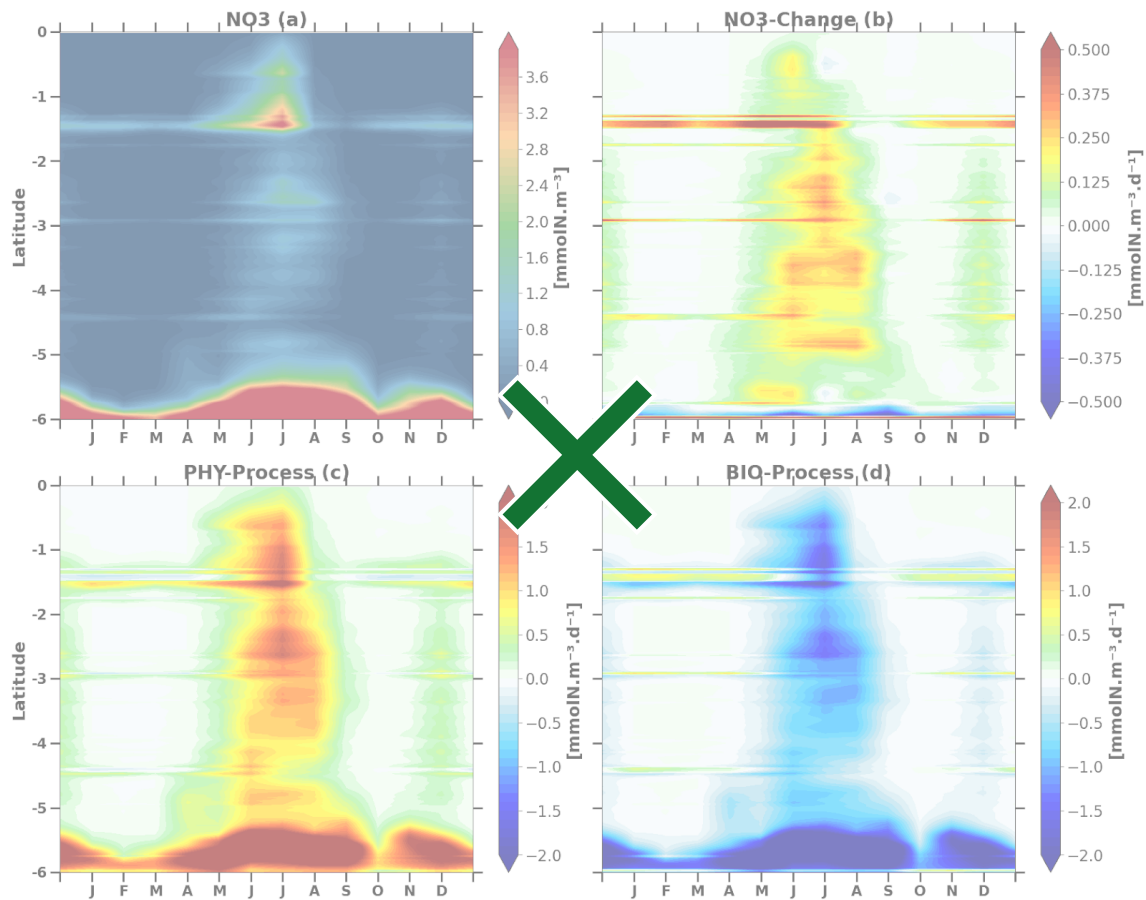
457

458 **Figure 6:** Seasonal cycle of surface current, zonal current (a, b) at  $10^\circ\text{E}$  section and between  $3^\circ\text{S}$  and  $7^\circ\text{S}$   
 459 meridional current (c, d) at  $4^\circ\text{S}$  section from  $7^\circ\text{E}$  to the coast.

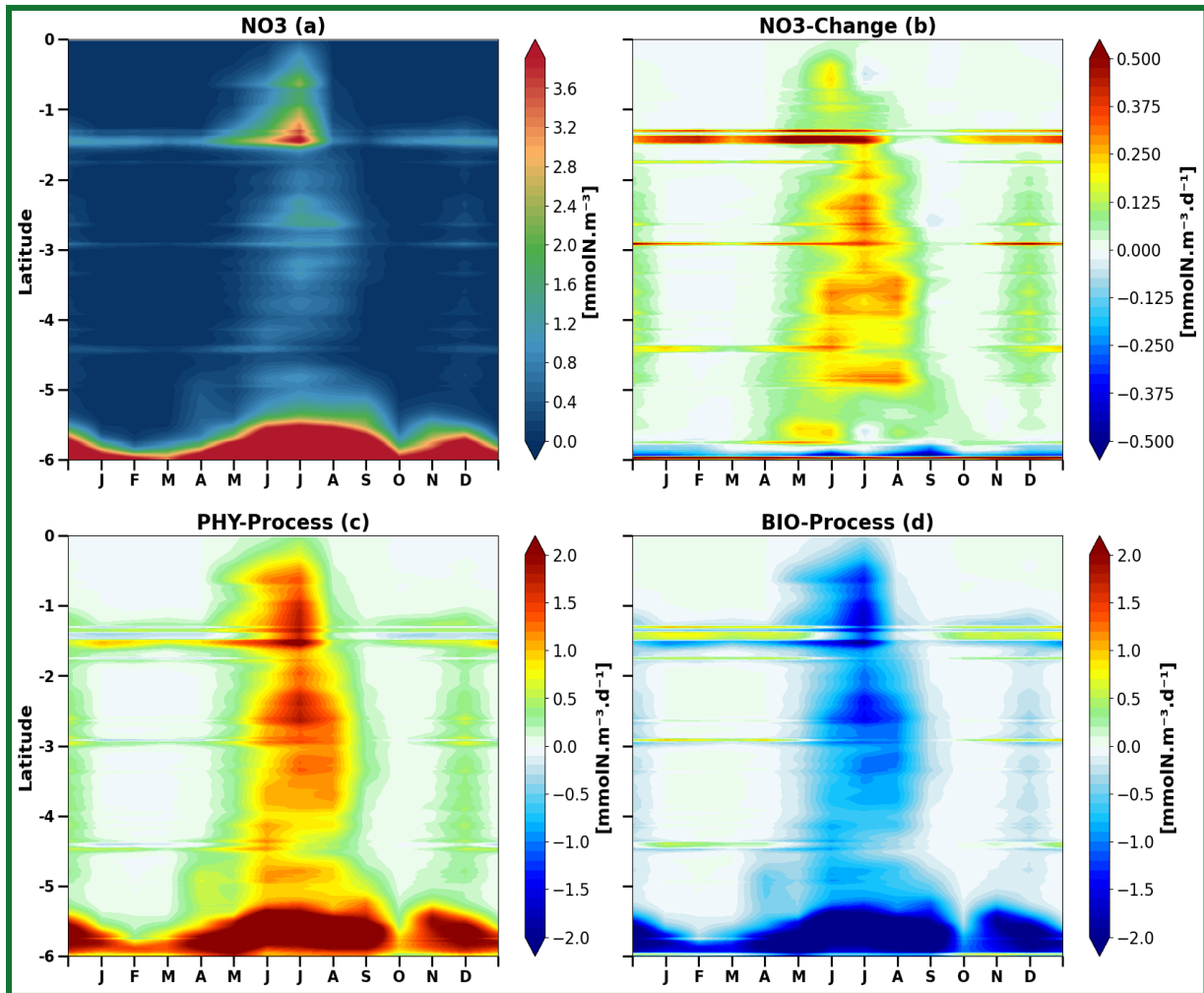
460 Then we have a weak second increasing phase in November-December of about  $0.1 \text{ mmol.m}^{-3}.\text{d}^{-1}$  and a  
461 weak decreasing phase in January- February ( $0.01 \text{ mmol.m}^{-3}.\text{d}^{-1}$ ) . This semi-annual cycle is due to a  
462 balance between nitrate supply by physical processes (Fig.7c), maximum during the main upwelling  
463 period, and nitrate consumption by biological processes (Fig.7d).

### 464 3.2.1 Seasonal Nitrate Budget Analysis: Horizontal Vs Vertical Contributions

465 Looking at our previous results, we saw that physical processes drive the nitrate supply in the  
466 Gabon-Congo upwelling system, now we will look at the contribution of horizontal and vertical  
467 processes to understand which are the main drivers for this nitrate supply. Fig.8 shows that horizontal  
468 and vertical processes (Fig.8a and Fig.8b respectively) are of great importance for nitrate supply.



469



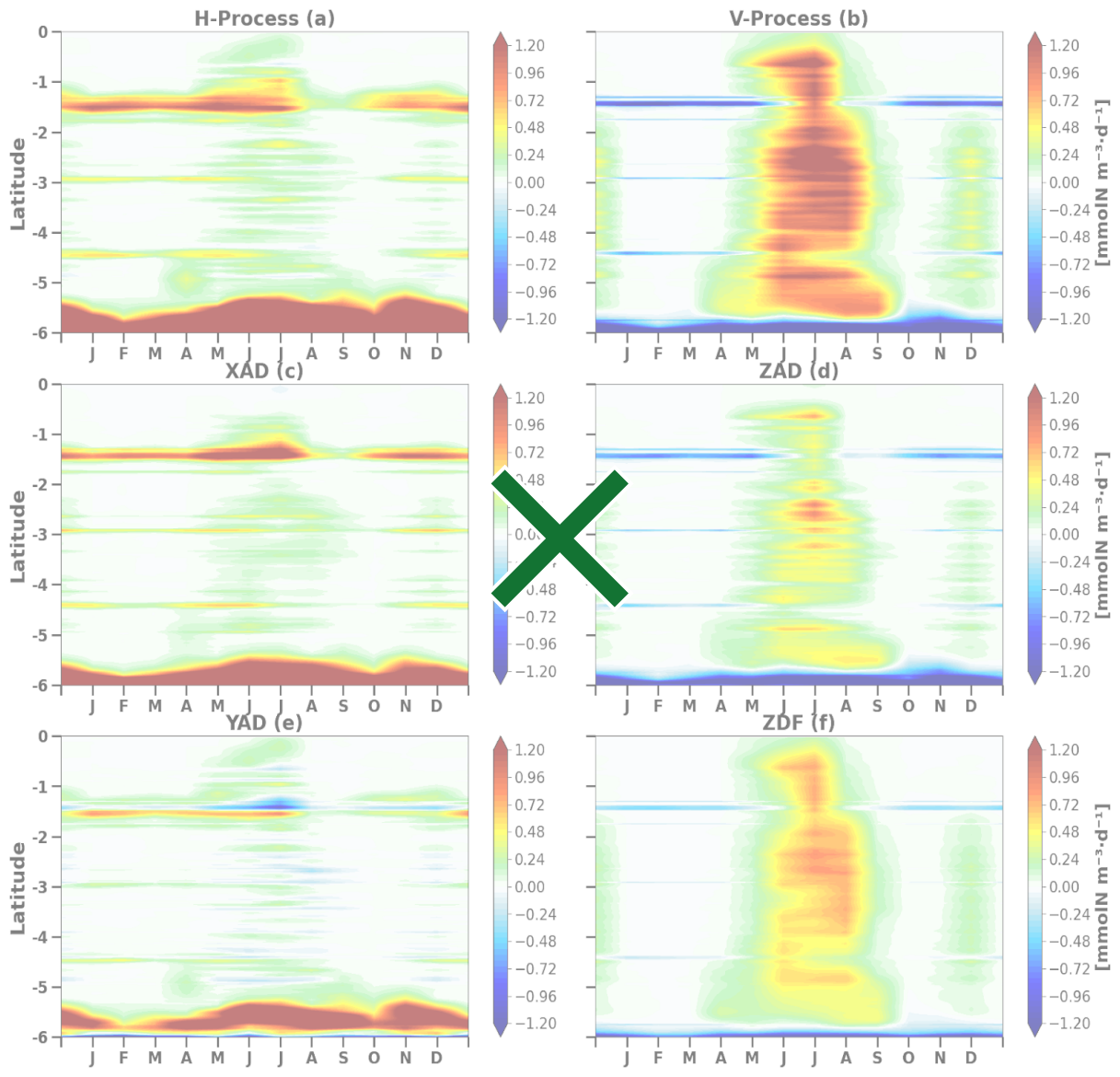
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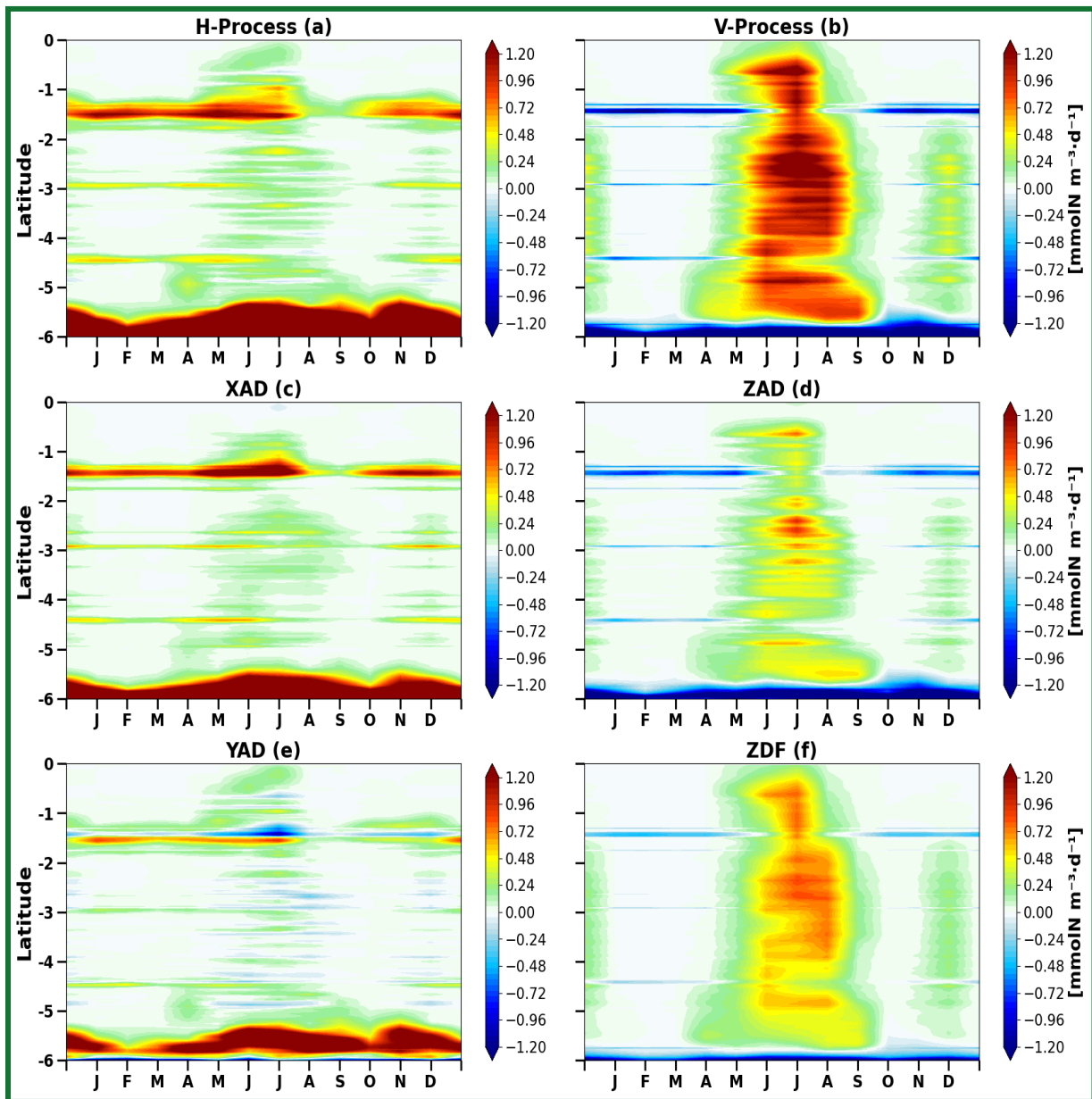
471 **Figure 7:** Latitude-time Hovmöller diagram of the model seasonal cycle of Mixed Layer Nitrate (MLN) budget,  
 472 a), the rate of the MLN change (b), the physical process contribution (c) and the biological process contribution  
 473 (d) along the Gabon-Congo coast. Units are  $\text{mmolN.m}^{-3}$  and  $\text{mmolN.m}^{-3}.\text{d}^{-1}$  for Figure 7a and Figure 7b,c,d,  
 474 respectively.

475 In fact, as we can see in the Fig.8, vertical processes (Fig.8b) are the main driver of nitrate supply  
 476 during the upwelling between  $0^{\circ}\text{S}$  and  $5.5^{\circ}\text{S}$  with an input magnitude of around  $1 \text{ mmol.m}^{-3}.\text{d}^{-1}$  along  
 477 the coast while the horizontal processes are the main driver at the vicinity of Congo river mouth ( $5.5^{\circ}\text{S}$   
 478 –  $6^{\circ}\text{S}$ ) all year long. The latter seems to be dominated by zonal advection (fig.8c) with a very high  
 479 nitrate input of more than  $1.2 \text{ mmolN.m}^{-3}.\text{d}^{-1}$  nearby  $6^{\circ}\text{S}$  with a northward extension, largest firstly in  
 480 November-December and secondly in June-July. This is consistent with the seasonal maximum of  
 481 Congo River discharge, which suggests a nitrate input through the river plume (Hopkins et al 2013).  
 482 North of  $6^{\circ}\text{S}$ , meridional advection (Fig.8e) drives horizontal processes.

483 The nitrate budget analysis reveals also that vertical processes (Fig.8b) are dominated by vertical  
 484 mixing (Fig.8f), while vertical advection has the same seasonality but a smaller contribution (Fig.8d).  
 485 Indeed, the nitrate input by the vertical diffusion is about  $0.7 \text{ mmolN.m}^{-3}.\text{d}^{-1}$  but only around  $0.5$   
 486  $\text{mmolN.m}^{-3}.\text{d}^{-1}$  by vertical advection. Both vertical processes decrease nitrate concentration nearby  
 487  $6^{\circ}\text{S}$ , under Congo River plume influence with the dominant zonal advection contribution. Indeed, as

488 nitrate concentration is greater in the near-surface Congo River plume than in subsurface (between 5 to  
489 10 m, see Fig.3), deeper waters rising at the surface by vertical advection reduce nitrate in the plume  
490 area.





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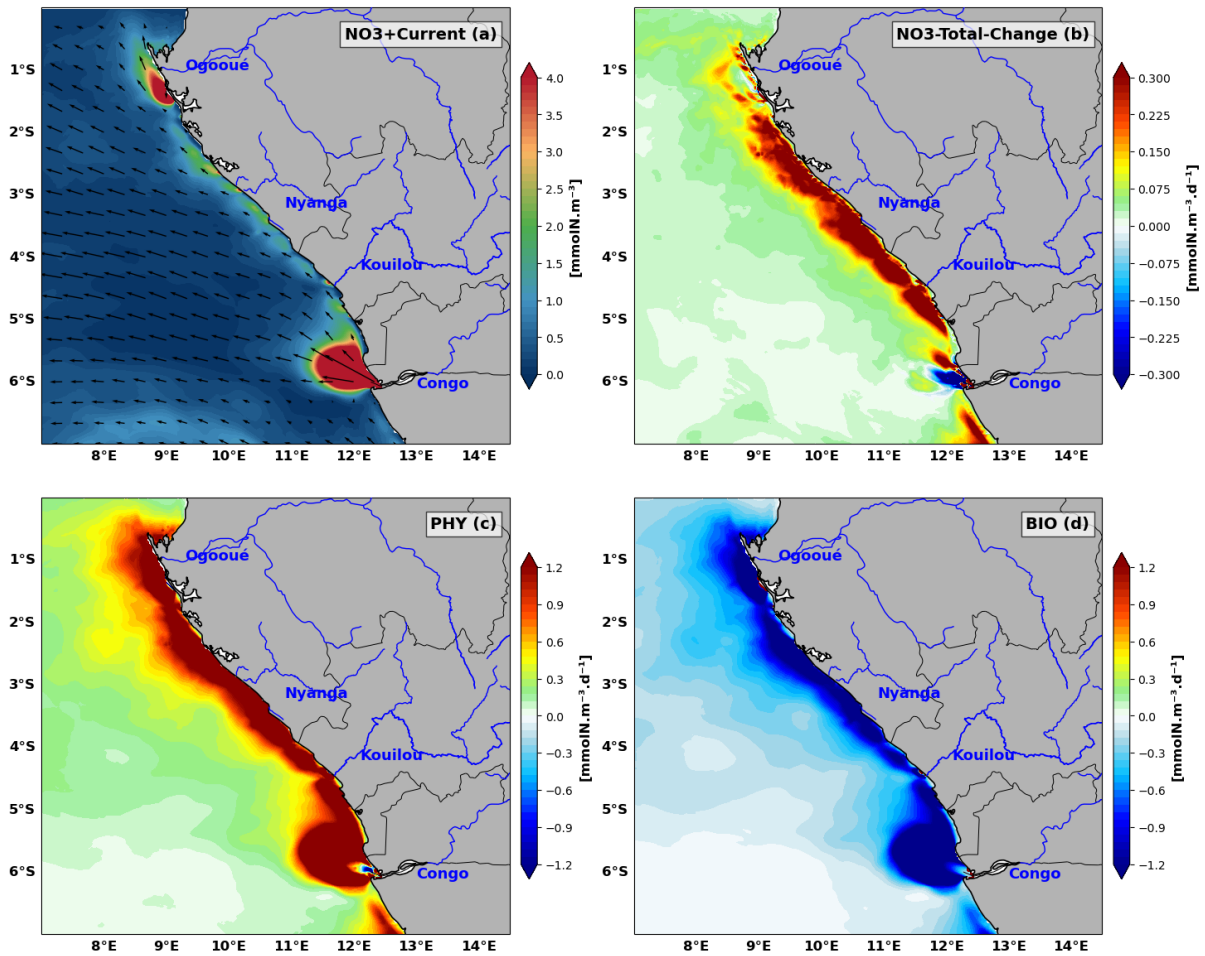
494 🌿

495 **Figure 8:** Latitude-time Hovmöller diagram of the model seasonal cycle of horizontal (a) and vertical (b) process  
 496 contributions , zonal (c), meridional (e), vertical (d) advectons , vertical diffusion (f) averaged in the mixed  
 497 layer along the Gabon-Congo coast. Units are  $\text{mmolN} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$ .

498 Similarly, vertical mixing of subsurface waters with the plume waters decreases nitrate concentration  
 499 at the surface, although the strong haline stratification associated with the Congo River plume limits  
 500 this effect.

501 It is important to note that, on the one hand, vertical advection (Fig. 8d) and vertical diffusion (Fig. 8f)  
 502 have the same seasonality as SLA (Fig. 4a), in opposite phase, northward of  $5.5^{\circ}\text{S}$ . This suggests that  
 503 the upwelling associated with CTWs (negative SLA) induce these vertical processes and therefore  
 504 drive the input of nitrate in the northern part of the Gabon-Congo coast. On the other hand, horizontal  
 505 advection (both zonal and meridional advectons) has the same seasonality as the Congo River

506 discharge between 5.5°S and 6°S. This suggests that the Congo River supplies nitrate through zonal  
 507 advection, near its mouth.



508

509 **Figure 9:** Spatial distribution averaged over the main upwelling period of (a) nitrate, (b) nitrate tendency  
 510 contributed by (c) physical processes and (d) biological processes, all averaged in the mixed layer in Austral  
 511 winter. The mean current in the mixed layer is superimposed in (a). Nitrate concentration units are  $\text{mmolN}\cdot\text{m}^{-3}$   
 512 and the tendency terms units are  $\text{mmolN}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ .

### 513 3.2.2 Regional Nitrate Budget Analysis in the main upwelling period: Physical Vs 514 Biological Contributions

515 The regional distribution of nitrate balance terms averaged over the mixed layer for the austral winter  
 516 (June-July-August), when upwelling reaches its maximum intensity, is presented in Fig.9. The nitrate  
 517 tendency (Fig.9b) shows that during the upwelling period, nitrate input occurs throughout the domain  
 518 with values varying between  $-0.3$  to  $0.3 \text{ mmolN}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$  in the plume zone and  $0.2$  to  $0.56$   
 519  $\text{mmolN}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$  along the coast in the northern part. In the offshore zone, the nitrate tendency is lower,  
 520 with a magnitude of around  $0.05 \text{ mmolN}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ . This distribution of the nitrate tendency shows that  
 521 the input of nitrate by physical processes (Fig.9c) is slightly greater than the uptake of nitrate by  
 522 biological processes (Fig.9d) throughout the area, explaining the positive nitrate change rate, except at

523 the Congo River mouth where we have negatives values . Fig.9a shows that nitrate inputs along the  
524 coast are very high close to river mouth and varies a lot along the coast over a width of about 165 km  
525 from the coast. During this main period of upwelling, in general, vertical processes (Fig. 10b) largely  
526 dominate the nitrate supply across the entire continental shelf. A continuous coastal band of strong  
527 enrichment is observed, with values often exceeding  $0.513$  to  $0.677$   $\text{mmolN.m}^{-2}.\text{d}^{-1}$ . Conversely,  
528 horizontal processes (Fig. 10a) show a more localized and overall lower contribution throughout the  
529 domain, with the notable exception of the Congo and Ogooué River mouth ( $\sim 6^\circ\text{S}$  and  $1^\circ\text{S}$   
530 respectively), where a massive positive flux (dark red,  $> 0.677$   $\text{mmolN.m}^{-2}.\text{d}^{-1}$ ) is observed.  
531 Comparing the spatial structure of the total horizontal process (Fig. 10a) with its individual  
532 components reveals a striking similarity to zonal advection (Xad, Fig. 10c). The Xad signal (Fig. 10c)  
533 almost perfectly reproduces the nitrate patch observed at the Congo mouth, indicating that zonal  
534 transport (east-west) is the main driver of horizontal nitrate injection into the mixed layer, associated  
535 with the offshore extension of the river plume. Although meridional advection (Yad, Fig. 10e) exhibits  
536 significant dipole structures near the Congo and patches along the coast, its intensity and spatial  
537 pattern provide a less compelling explanation for the overall horizontal process signal. It can therefore  
538 be concluded that zonal advection is the dominant term dictating the distribution of horizontal fluxes  
539 in this region. The study of vertical components shows that the total vertical process (Fig. 10b) results  
540 from two distinct yet complementary mechanisms. Vertical advection (Zad, Fig. 10d) shows very  
541 intense ( $> 0.677$   $\text{mmolN.m}^{-2}.\text{d}^{-1}$ ) but highly localized supply along the coastline and capes,  
542 representing the typical signature of coastal upwelling driven by wind and Coastally Trapped Waves  
543 (CTWs). However, vertical diffusion (Zdf, Fig. 10f) shows the strongest resemblance to the overall  
544 Vert\_Process. It exhibits a broad and homogeneous distribution extending well offshore from the coast,  
545 with sustained values between  $0.349$  and  $0.513$   $\text{mmolN.m}^{-2}.\text{d}^{-1}$ . Unlike advection, which is highly  
546 segmented, vertical diffusion better explains the spatial continuity of nitrate supply across the shelf.  
547 This suggests that while advection (upwelling) brings nitrate to the base of the mixed layer, turbulent  
548 mixing (diffusion) ensures its effective distribution toward the surface across the entire domain. ▀

### 549 3.3 Nitrate budget in the euphotic layer and along the water column

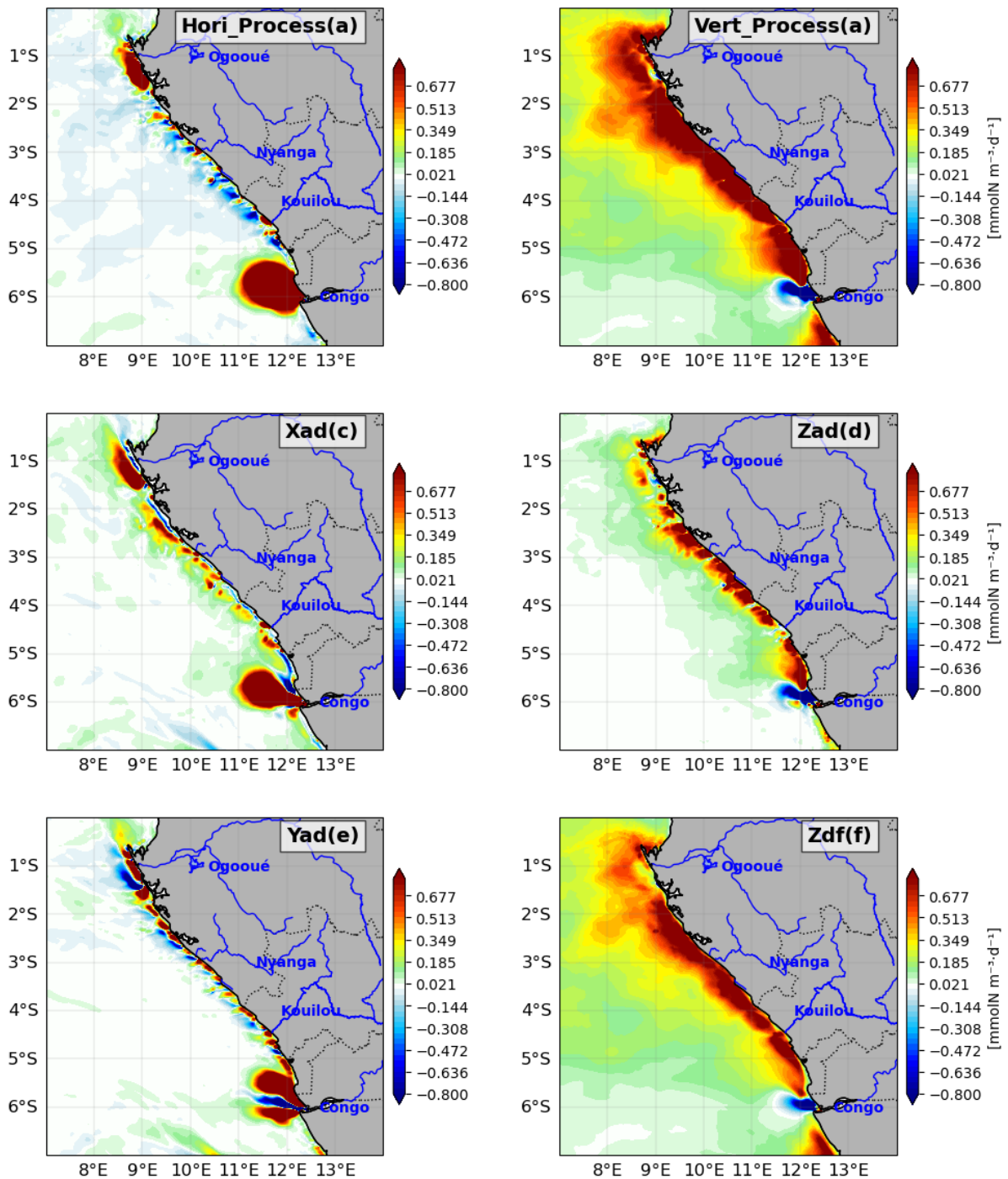
550 Now, in addition to the processes acting in the surface mixed layer, we investigate other processes  
551 involved in the nitrate budget below the mixed layer by analysing the nitrate budget in the euphotic  
552 layer, generally defined as the zone where light penetration exceeds 1% of the surface light, allowing  
553 for the presence of phytoplankton and other photosynthetic organisms. The seasonal variations of  
554 thermocline, mixed layer and euphotic layer depths are compared in Fig.11. In Fig.11a, the  
555 thermocline ( $20^\circ\text{C}$  isotherm) variation is very close to the nitracline as suggested by Radenac et al  
556 (2020). The mixed layer euphotic layer is very shallow ( $\sim 10$  m) throughout the year probably due to  
557 the Congo River plume stratification. The euphotic layer extends deeper than the mixed layer, but is  
558 generally shallower than the thermocline, except from June to September. The euphotic layer gets

559 thinner during upwelling through the enhancement of CHLa concentration which reduces light  
560 penetration (self-shadowing by CHLa). Overall the nitrate tendency (Fig.11b) has the same  
561 semi-annual variation in the euphotic layer than in the mixed layer, although more intense in the  
562 euphotic layer with a maximum at the bottom of the euphotic layer. In fact, most nitrate input by  
563 physical processes (Fig.11c) happens in the mixed layer, where it is almost balanced by biological  
564 nitrate uptake (Fig.11d). In contrast, in the euphotic layer below the mixed layer (between 10m and  
565 40m depth), biological processes are poorly active and the nitrate variability is almost exclusively  
566 induced by physical processes. The mean nitrate input in the euphotic layer is about  $0.1 \text{ mmolN.m}^{-3}.\text{d}^{-1}$   
567 during the main upwelling period and the maximum input ( $0.2 \text{ mmolN.m}^{-3}.\text{d}^{-1}$ ) occurs in May at the  
568 base of the euphotic layer (Fig.11b).

569 In the euphotic layer, biological activity is dominated by photosynthesis which removes nitrate,  
570 whereas below the euphotic layer remineralization supplies nitrate with about  $0.05 \text{ mmolN.m}^{-3}.\text{d}^{-1}$   
571 almost all year long (Fig. 11d).

### 572 3.3.1 Euphotic Layer Nitrate Budget Analysis: Horizontal Vs Vertical Contributions

573 Fig.12 shows that, even in the euphotic layer, the physical contribution to nitrate supply (Fig.11c) is  
574 mostly driven by vertical processes (Fig.12b). However, the large decrease in nitrate (Fig.11b) in  
575 October is also caused by horizontal contributions (Fig.12a) in the euphotic layer. Between the surface  
576 and 5m depth, horizontal processes dominate nitrate input (Fig.12e). In the euphotic layer below,  
577 meridional advection is the main driver of nitrate removal almost year-round, particularly in June and  
578 October.

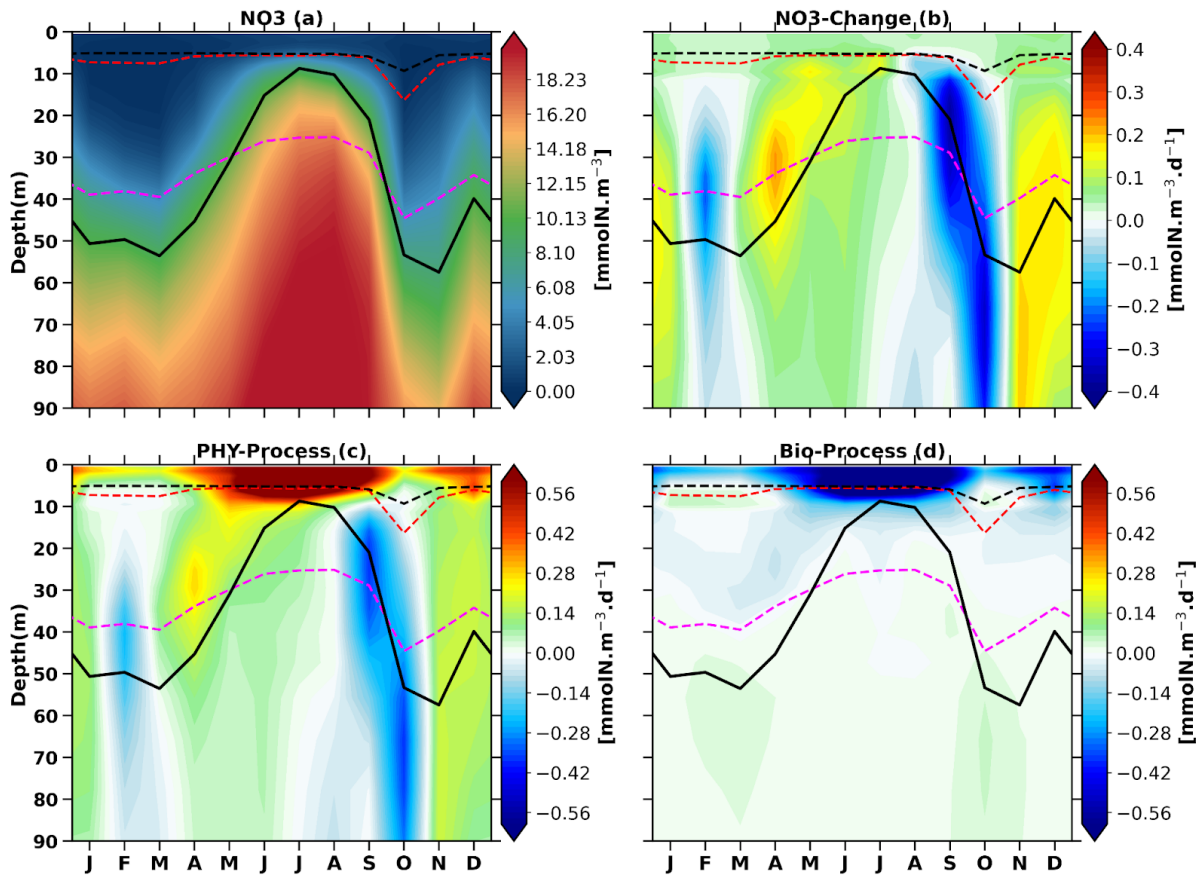


579

580 **Figure 10:** Contribution of (a) the horizontal processes, including (c) zonal advection and (e) meridional  
 581 advection, and (b) vertical processes, including (d) vertical advection and (f) vertical diffusion, to the nitrate  
 582 budget averaged in the mixed layer during the austral winter. Units are  $\text{mmolN} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$ .

583 Zonal advection (Fig.12c) supplies nitrate in the euphotic layer, with a maximum above the mixed  
 584 layer depth, throughout the year. This nitrate input is more than compensated by nitrate lost by  
 585 meridional contribution, below the upper 5 m (Fig.12e), except in June, July and August. Vertical  
 586 advection (Fig.12d) is the dominant vertical process (Fig.12b) in the nitrate budget. Below 30 m depth,  
 587 it has a semi-annual cycle characteristic of upwelling and downwelling CTWs propagation, associated

588 with nitrate increase when the thermocline shallows and nitrate decrease when the thermocline  
 589 deepens, with the maximum and minimum values around the thermocline depth. Moreover, vertical  
 590 advection supplies more nitrate in the mixed layer than in the euphotic layer below during the main  
 591 upwelling period (June, July and August), but rather the opposite during the second upwelling period  
 592 (December). Between the mixed layer depth and the euphotic layer depth, vertical diffusion (Fig.12f)  
 593 tends to partially compensate for the effects of vertical advection on nitrate. However, in the mixed  
 594 layer it mostly supplies nitrate, particularly during the upwelling seasons.



595

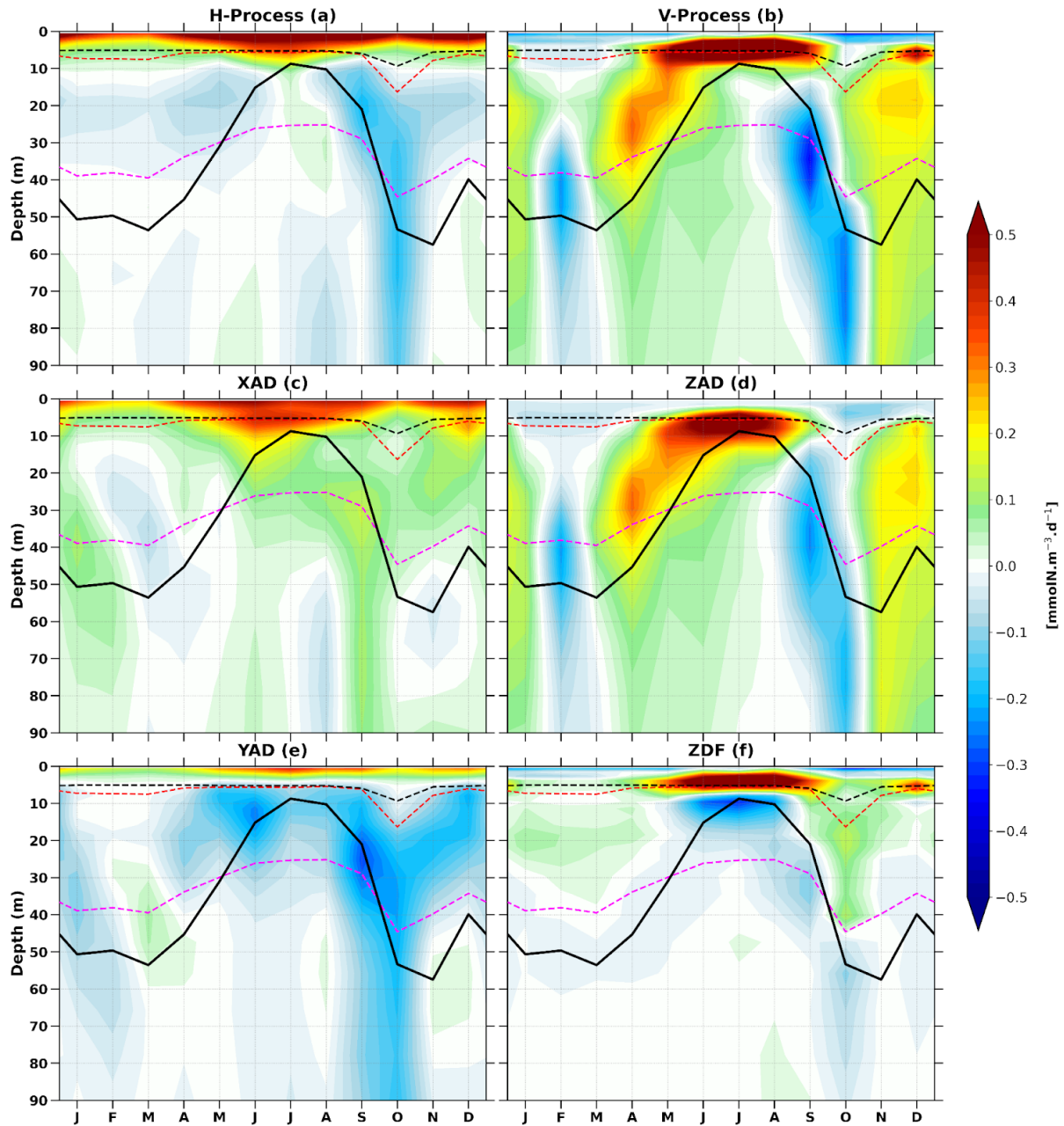
596 **Figure 11:** Depth-time Hovmöller diagram of the seasonal cycle of the nitrate budget averaged within the  
 597 Gabon-Congo coastal box ( $0^{\circ}\text{S}$ – $6^{\circ}\text{S}$ ,  $1^{\circ}$  wide coastal band, as shown in Fig. 1). (a) Nitrate concentration  
 598 ( $\text{mmolN.m}^{-3}$ ), (b) nitrate rate of change, (c) physical process contribution, and (d) biological process  
 599 contribution ( $\text{mmolN.m}^{-3}.\text{d}^{-1}$ ). The black solid line represents the thermocline ( $20^{\circ}\text{C}$  isotherm), while dashed  
 600 magenta, red and black lines indicate the euphotic, isothermal and mixed layer depths, respectively.

### 601 3.3.2 Nitrate budget analysis: advection components analysis

602 As nitrate advection depends on velocity and on the nitrate gradient, we now evaluate the individual  
 603 contributions of seasonal variations in velocity and nitrate gradient, as well as their combined effect, to  
 604 the seasonal variations of nitrate advection (see section 2.3, equation 4).

#### 605 3.3.2.1 Nitrate budget analysis: horizontal advection

606 Fig.13 allows to visually compare the depth-time structure of the zonal nitrate advection (Fig.13a)  
 607 with that of its different components, while correlation  $r$  is used to quantify the comparison.

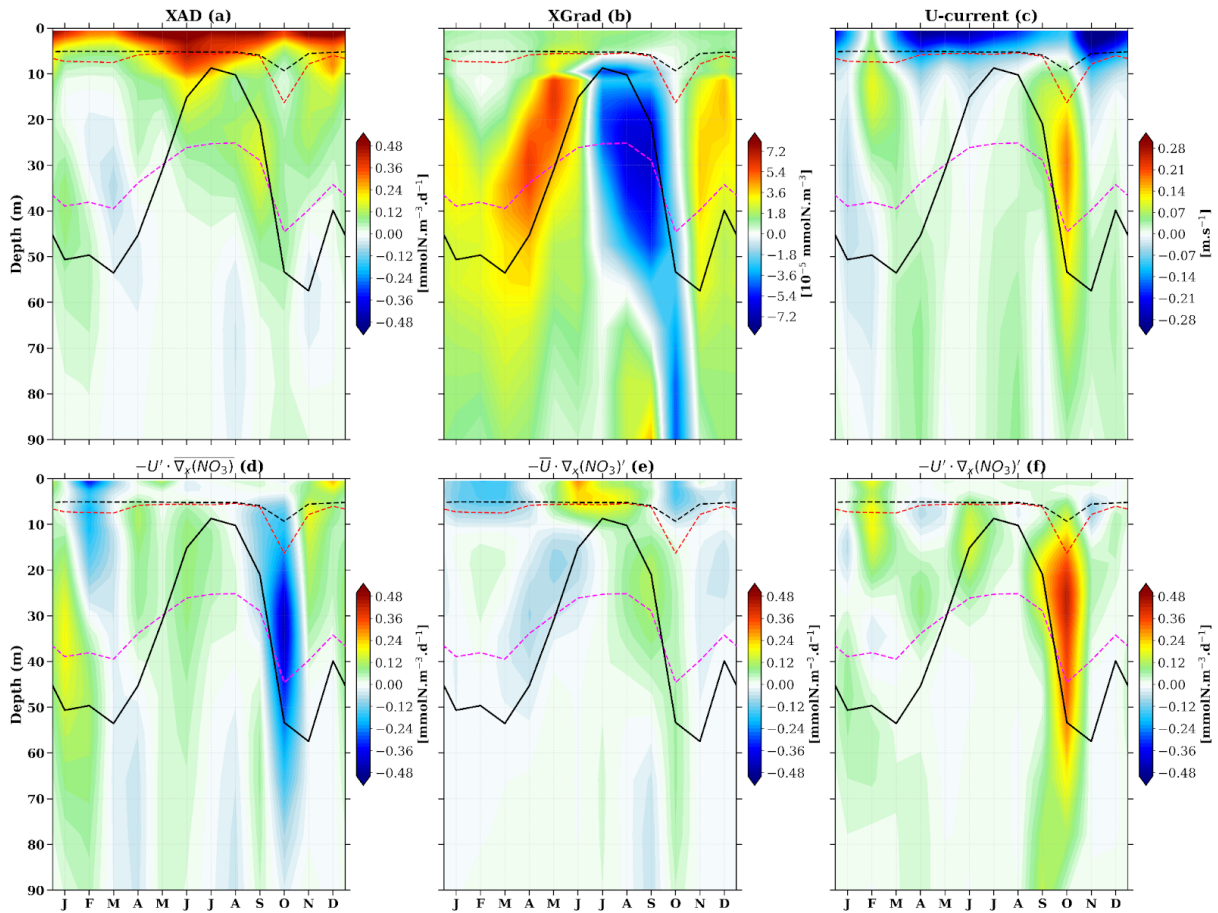


608

609 **Figure 12:** Depth-time Hovmöller diagram of the model seasonal cycle of contributions to the nitrate budget of  
 610 horizontal and vertical processes (a and b respectively), zonal, meridional, vertical advections (c, e and d  
 611 respectively), vertical diffusion (f) along the Gabon-Congo coast (0°S-6°S and 1° width to the coast). Units are  
 612  $\text{mmolN.m}^{-3}$  for all of the plots. The black solid line represents the thermocline (20°C isotherm), while dashed  
 613 magenta, red and black lines indicate the euphotic, isothermal and mixed layer depths, respectively.

614 The seasonal cycle of zonal nitrate advection in the 0-100 m water column (Fig. 13a) is controlled first  
 615 by the term  $\overline{u \cdot \nabla x(NO_3)}$  (Fig.13e,  $r=0,77$ ,  $p<0,05$ ), i.e. the annual mean zonal current multiplied by  
 616 the seasonal variations of the nitrate zonal gradient, second by the term  $u \cdot \overline{\nabla x(NO_3)}$ , (Fig.13d,  $r=0,49$ ,  
 617  $p<0,05$ ), i.e. the seasonal variations of the zonal current multiplied by the annual mean nitrate zonal  
 618 gradient, and third (and much less) by the term. The third component, which represents the

619 simultaneous variation in zonal current and nitrate gradient  $u' \cdot \nabla_x(NO_3)'$ , (Fig.13f,  $r=-0,15$ ,  $p<0.05$ ),  
 620 i.e. the product of seasonal variations of both the zonal current and the nitrate zonal gradient. The  
 621 seasonality of the zonal current (Fig. 13c) is influenced by the seasonal cycle of the South Equatorial  
 622 Undercurrent (SEUC), with maximum values in September-October and February-March (Dorothee et  
 623 al, 2004) in this zone ( $0^\circ\text{S}-6^\circ\text{S}$ ,  $1^\circ$  from the coast). Thus we can conclude that the SEUC plays a key  
 624 role in the nitrate balance in the Gabon-Congo system by bringing nitrate in February-March and in  
 625 September-October to the euphotic layer.



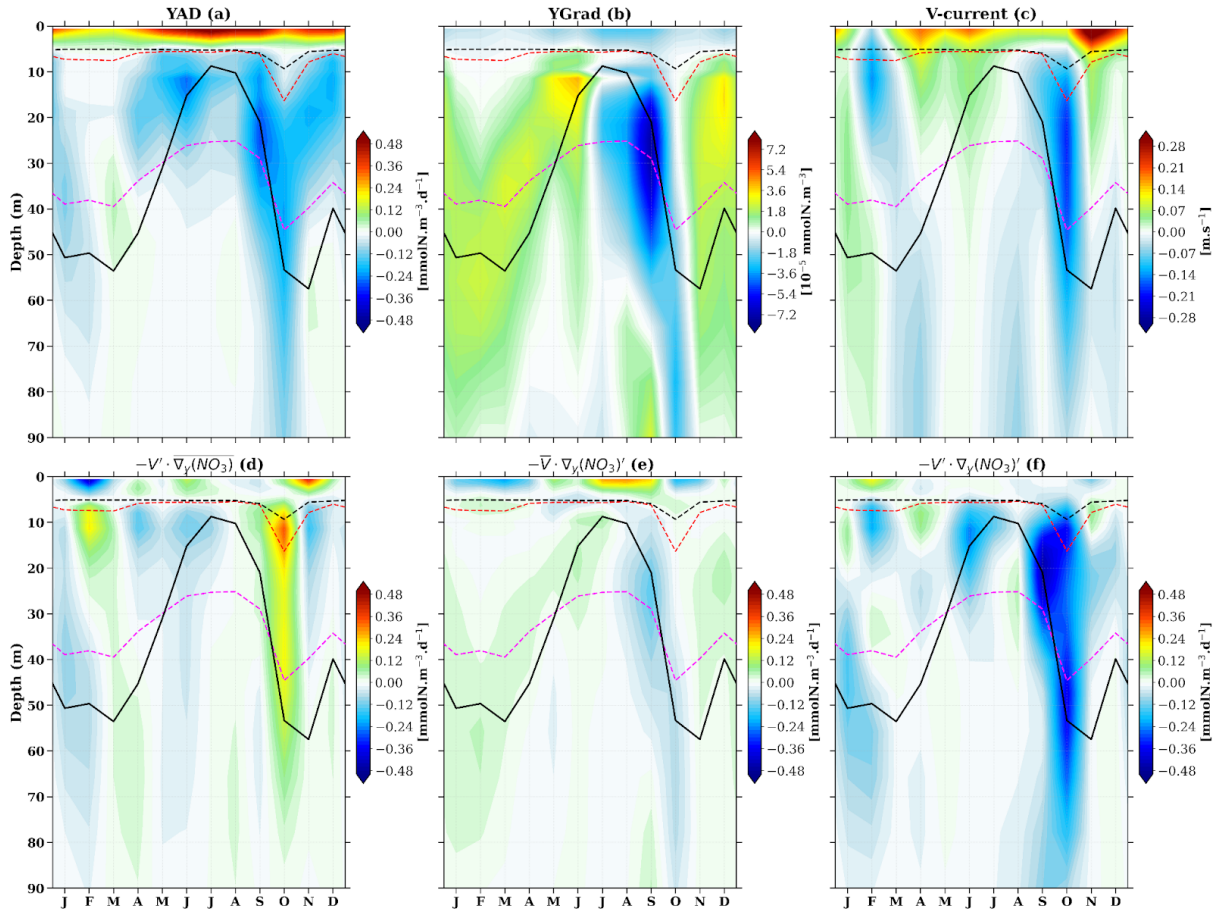
626  
 627 **Figure 13:** Depth-time Hovmöller diagram of the model seasonal cycle of nitrate advection (a), nitrate gradient  
 628 (b), zonal current (c), zonal current variation times mean nitrate gradient (d), gradient variation times mean  
 629 current (e) and gradient variation times zonal current variation (f), all along the zonal axis in the Gabon-Congo  
 630 coastal box of Fig. 1. Units are milli mol per cubic meter per day for all of the plots except (b) (milli mol per  
 631 cubic meter) and (c) (meter per second). The black solid line represents the thermocline ( $20^\circ\text{C}$  isotherm), while  
 632 dashed magenta, red and black lines indicate the euphotic, isothermal and mixed layer depths, respectively.

633 In the euphotic layer, we see that, as for the meridional nitrate advection, the meridional current  
 634 (Fig.14c) looking at the shape seems to be the main factor in the vertical and temporal variation shape  
 635 of the meridional nitrate advection (Fig.14a). The Angola current (AC), is the factor which modulates  
 636 nitrate lost by meridional nitrate advection throughout the year, with maximum loss in  
 637 September-October and June-July, in and below the euphotic layer, except in the first 5 m-depth.

638 Our analysis in this section reveals that the simultaneous variation in both the meridional current and  
639 the gradient ( $v' \cdot \nabla_y(NO_3)$ ), Fig.14f) exhibits the highest correlation ( $r=0.527$ ,  $p<0.05$ ) with meridional  
640 nitrate advection, thus explaining the major changes in advection. This result highlights the significant  
641 impact of the concurrent variability of both meridional current and gradient on meridional nitrate  
642 advection in the euphotic layer. In contrast, gradient variation ( $\overline{v' \cdot \nabla_y(NO_3)}$ ), Fig.14e) is poorly  
643 correlated ( $r=0.97$ ,  $p<0.05$ ) with meridional nitrate advection. The very low positive correlation with  
644 total meridional advection (a) indicates this term, representing the effect of a mean meridional current  
645 acting on a fluctuating nitrate gradient. This suggests that either the mean meridional current is weak,  
646 or its interaction with the fluctuating gradient does not lead to significant changes in overall advection.  
647 The variation in the meridional current ( $v' \cdot \overline{\nabla_y(NO_3)}$ ), Fig.14d) shows the lowest correlation ( $r=0.287$ ,  
648  $p<0.05$ ). This low, negative correlation with total meridional advection (Fig.14a) indicates that this  
649 term, representing the effect of fluctuating meridional currents on a relatively stable mean nitrate  
650 gradient, is not a dominant driver of the overall meridional nitrate advection. In fact, a negative  
651 correlation suggests it might weakly oppose the main advection pattern or have an inverse relationship.  
652 This implies that the mean gradient is either small or the meridional current variations are not aligned  
653 to produce significant advection changes via this mechanism.

### 654 3.3.2.2 Nitrate budget analysis- vertical processes

655 Our analysis reveals that within the euphotic layer, the variation in the vertical gradient  $\overline{w' \cdot \nabla_z(NO_3)}$ ,  
656 Fig.15e) appears to better explain the variation in vertical nitrate advection (Fig.15a), showing a  
657 correlation of  $r=0.79$  ( $p<0.05$ ). In contrast, vertical velocity variation ( $w' \cdot \overline{\nabla_z(NO_3)}$ ), Fig.15d) plays a  
658 secondary role, with a correlation of approximately 0.646 ( $p<0.05$ ) with vertical nitrate advection.  
659 Looking now at the vertical nitrate advection, we can see strong similarities in the vertical and  
660 temporal variation structure between vertical advection seasonality (Fig.15a), vertical nitrate gradient  
661 seasonality (Fig.15b) and vertical velocity seasonality (Fig.15c), both three are very strong in the  
662 euphotic layer. We can also see in the semi-annual vertical velocity that from April to August and  
663 November-December, vertical velocities are upward corresponding to negative values of SLA (Fig.4a,  
664 4b), lowest SST (Fig.4c, 4d) values and highest nitrate concentration (Fig.4e, 4f). From January to  
665 March and September-October, vertical velocities are downward corresponding to positive values of  
666 SLA (Fig.4a, 4b), highest SST (Fig.4c, 4d) values and lowest nitrate concentration (Fig.4e, 4f). This  
667 later observation confirms that CTWs propagating from April to August and November-December are  
668 associated with upwelling. In contrast, CTWs propagating from January to March and  
669 September-October are associated with downwelling. Note that similar results were found by Ngakala  
670 et al. (2025) for the seasonal heat budget in the Gabon-Congo upwelling (from 4°S-6°S and 1° width  
671 to the coast) and also further south in the Angolan upwelling by Korner et al. (2024).



672

673 **Figure 14:** Depth-time Hovmöller diagram of the model seasonal cycle of nitrate advection (a), nitrate gradient  
 674 (b), meridional current (c), meridional current variation times mean nitrate gradient (d), gradient variation times  
 675 mean meridional current (e) and gradient variation times current variation (f), all along the meridional axis in the  
 676 Gabon-Congo coastal box of Fig. 1b. Units are milli mol per cubic meter per day for all of the plots except (b)  
 677 (milli mol per cubic meter) and (c) (meter per second). The black solid line represents the thermocline (20°C  
 678 isotherm), while dashed magenta, red and black lines indicate the euphotic, isothermal and mixed layer depths,  
 679 respectively.

680 However, if we average in the first hundred meters, vertical velocity variation has the highest  
 681 correlation of 0.831 ( $p < 0.05$ ) with vertical advection, whereas vertical gradient variation has only 0.63  
 682 ( $p < 0.05$ ) of correlation with vertical advection. The third component ( $w' \cdot \nabla_z(NO_3)'$ ), Fig.15f) has a  
 683 lower negative correlation -0.062 ( $p < 0.05$ ) with vertical advection. During the upwelling period, the  
 684 variation in vertical gradient (Fig.15e) at the base of the mixed layer has a much greater influence on  
 685 nitrate supply than the variation in vertical velocity (Fig.15e). Another observation is that in the same  
 686 main upwelling period there is a lag between maximum vertical current which happens in May and the  
 687 maximum vertical gradient indicated by the shallowest thermocline in July. This lag results in a  
 688 highest input of nitrate by vertical advection (Fig.15a) in the mixed layer in June. It can be seen that  
 689 the nitrate output by vertical advection during the downwelling period is mostly induced by the

690 vertical nitrate gradient in the mixed layer whereas deeper in the euphotic layer these losses are  
691 induced by vertical downward velocities induced by downwelling CTWs propagation.

#### 692 **4 Discussion**

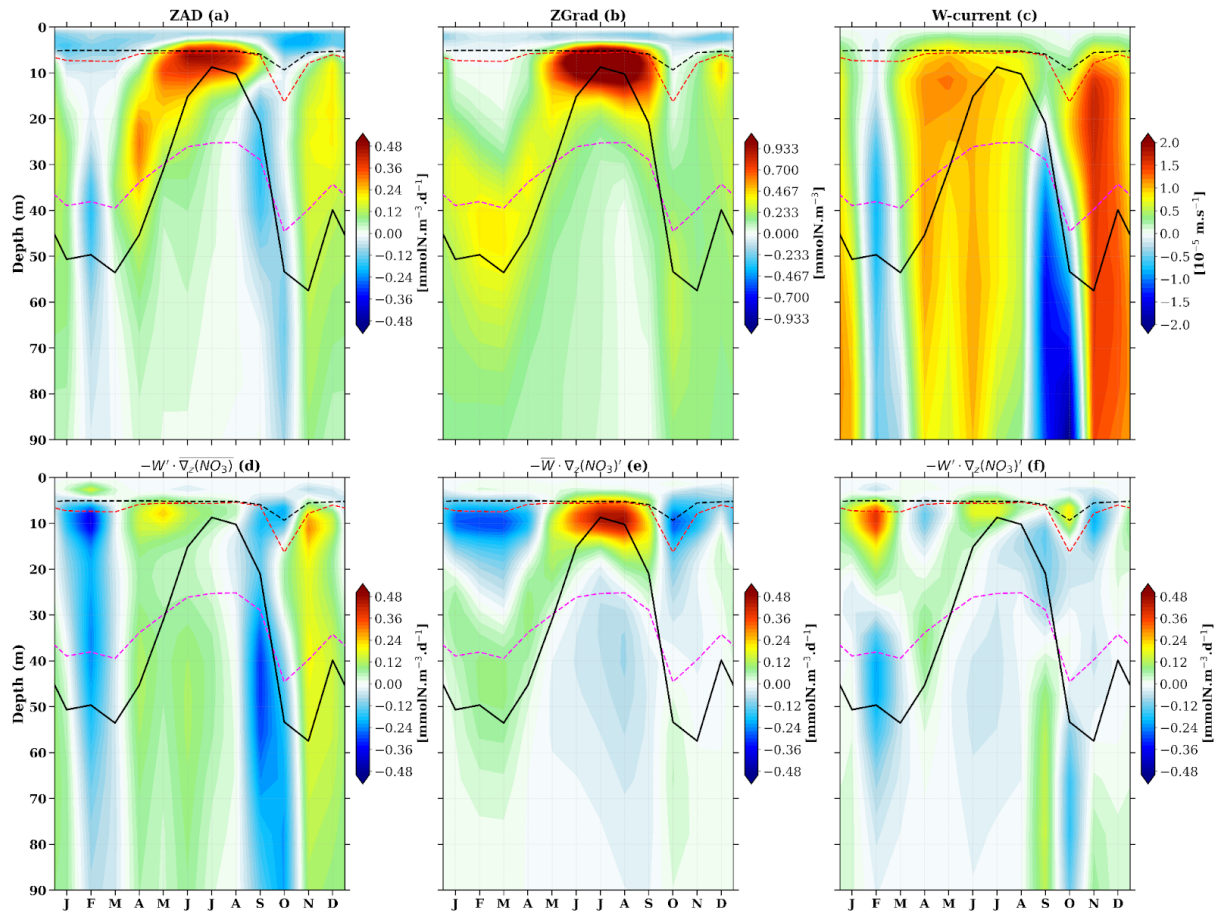
693 In this section, we discuss our results: the model-data comparison, the influence of the mixed layer  
694 criteria, the main nitrate budget drivers in the Gabon-Congo upwelling system compared to the other  
695 tropical Atlantic upwelling systems. Finally, we will explore the factors governing seasonal  
696 productivity in the Gabon-Congo upwelling system, integrating our understanding of physical forcing  
697 and nutrient availability to characterize its biological response. Through this comprehensive  
698 discussion, we aim to provide a nuanced understanding of the oceanographic processes at play in the  
699 coastal Congo region and the capabilities and limitations of our modeling approach.

700 Throughout this work, we have shown that our model reasonably reproduces the observations in terms  
701 of temperature, nitrate, CHL<sub>a</sub>, SLA and surface currents, although there are a few differences that we  
702 will discuss in this section. First of all, we saw that temperature in our model is warmer than observed  
703 by around 1°C in regional distribution (Fig. 2a,b) as well as in seasonal cycles (Fig. 4c,d). This is a  
704 common bias in ocean and climate models in the Eastern tropical Atlantic (Richter, 2015; Zuidema et  
705 al., 2016; Voltaire et al., 2019). Indeed, several studies suggest that this warm bias is multicausal.  
706 While it is partly attributed to models' deficiency in simulating low-level clouds, resulting in  
707 overestimation of shortwave radiation (Xu et al., 2014), other factors play a critical role. These include  
708 errors in atmospheric forcing, specifically the misrepresentation of the coastal low-level jet and wind  
709 stress, which can weaken coastal upwelling (Cabos et al., 2017; Voltaire et al., 2019). Furthermore,  
710 complex air-sea feedback mechanisms (Koseki et al., 2018) and difficulties in simulating the vertical  
711 thermocline structure in the region (Koubanova et al., 2018) are also shared challenges that contribute  
712 to this persistent modeling bias.

713

714

715



716

717 **Figure 15:** Depth-time Hovmöller diagram of the model seasonal cycle of nitrate advection (a), nitrate gradient  
 718 (b), vertical current (c), vertical current variation times mean nitrate gradient (d), gradient variation times mean  
 719 vertical current (e) and gradient variation times current variation (f), all along the vertical axis in the  
 720 Gabon-Congo coastal box of Fig. 1b. Units are milli mol per cubic meter per day for all of the plots except (b)  
 721 (milli mol per cubic meter) and (c) (meter per second). The black solid line represents the thermocline (20°C  
 722 isotherm), while dashed magenta, red and black lines indicate the euphotic, isothermal and mixed layer depths,  
 723 respectively.

724 With regard to nitrate concentrations, the regional distribution shows that north of the mouth of the  
 725 Congo River and near the coast, the model agrees well with the CARS climatology (Fig. 2c,d).  
 726 However, offshore and south of the mouth of the Congo River, the model underestimates nitrate  
 727 concentrations. In the seasonal cycle, we see that the model captures the seasonal variability, but  
 728 underestimates the amplitude compared to the data. These biases may be explained by the temporal  
 729 coverage of the CARS climatology, which covers a long period (from 1940 to 2011) of data  
 730 (Bachelery et al., 2016) compared to our model which covers only one year (2011). Another bias may  
 731 be the lack of data in CARS, in our study area. The differences in the surface CHLa concentration  
 732 between the model and the satellite observations may be associated with a lack of data for the ocean  
 733 colour satellite observations, particularly in August, due to the cloud cover which induces atmospheric  
 734 contaminations (Hardman-Mountford and McGlade., 2002; Estival et al., 2013) of the satellite signal,

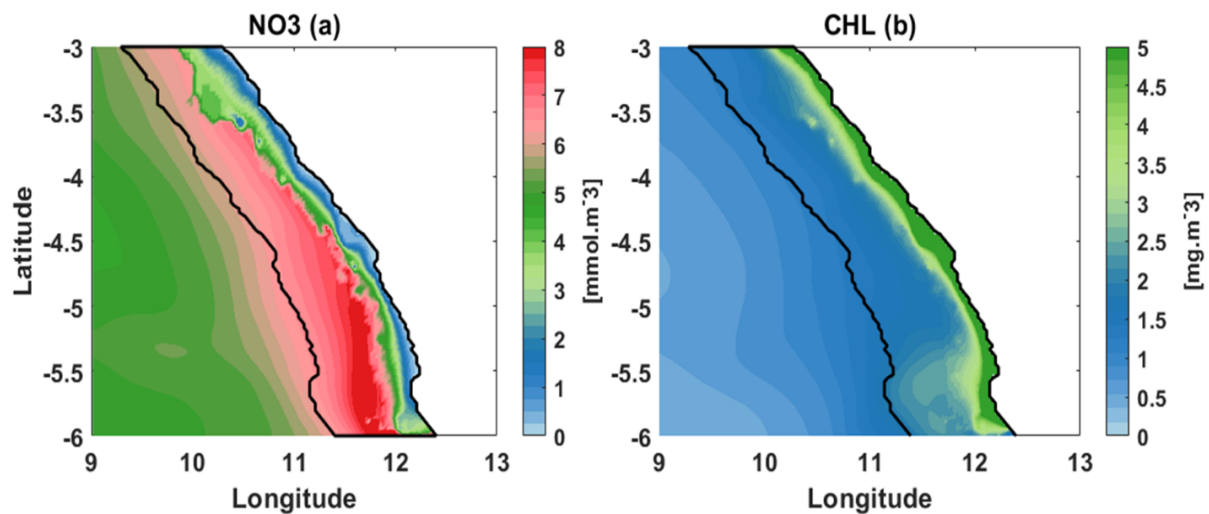
735 resulting in a lack of CHLa signal (Nieto et al., 2016). The biases in the surface currents between the  
736 model and the observations are mainly due to the underestimation of the currents in the OSCAR  
737 product near the coastal zone (Sikhakolli et al., 2013), especially in our studied area where very few  
738 data are available. Despite these results discussed earlier in this paper, we have to keep in mind that  
739 there are also some limitations in our simulation. For example, the model has difficulties reproducing  
740 the seasonal cycle of CHLa concentration, in particular the first CHLa blooms occurring in  
741 February-March, highlighted by the MODIS ocean colour satellite data. This might be due to the  
742 CHLa concentration of the Congo river in our model. Indeed, we take into account the nutrients and  
743 dissolved organic matter discharges of the river but not the CHLa concentrations (information not  
744 available in the HYBAM database). We can also observe a minimal or slightly reduced concentration  
745 of CHLa around the mouth of the Congo River in our model (Fig. 2e). This is explained by the very  
746 high speed (greater than 2 m/s) of the Congo River current at its mouth in our model. This has resulted  
747 in the transport of CHLa produced by phytoplankton photosynthesis away from the mouth of the  
748 Congo River.

749 Our analysis shows that, in the Gabon-Congo upwelling system, the nitrate budget in the mixed layer  
750 is dominated by physical processes during the upwelling period (Fig. 7c), particularly vertical  
751 diffusion (Fig. 8f), while zonal advection and vertical mixing play a secondary role. In agreement to  
752 these latter results, Ngakala et al. (2025) using a high resolution simulation ( $1/36^\circ$ ) of NEMO in the  
753 Gabon-Congo upwelling, have shown through a mixed layer heat budget, that vertical diffusion was  
754 the main contributor of cooling during upwelling period in the mixed layer. They found that the  
755 vertical advection has a secondary role in cooling of the mixed layer. They state that, if defining  
756 instead the mixed layer depth with the Boyer-Montégut criterion, then vertical advection would play a  
757 greater role than vertical diffusion. Thus, as mentioned in our study and in agreement with Ngakala et  
758 al. (2025), the relative contributions of vertical advection and diffusion depend on the definition of the  
759 mixed layer depth.

760 Our analysis reveals that the seasonal variability of CHLa in our region is driven by the seasonal  
761 concentration of nitrate, as in other tropical Atlantic upwelling systems (Radenac et al., 2020).  
762 However different processes drive the seasonal cycle of nitrate and CHLa in the different tropical  
763 Atlantic upwelling systems. In the Equatorial Atlantic upwelling system, the seasonal cycle of nitrate  
764 and CHLa are driven by the wind stress and wind stress curl (Caniaux et al., 2011, Radenac et al.,  
765 2020). In the Tropical Angola Upwelling system, the main driver of these seasonal cycle are the CTWs  
766 as in our area with a main peak in austral winter (May-July) and a second peak in December-January.  
767 However vertical mixing plays also a key role in the Tropical Angola Upwelling system (Awo et al.,  
768 2022; Ostrowski et al., 2009; Körner et al., 2023) due to onshore propagating internal tide waves  
769 interacting with sloping topography (Brandt et al., 2023). In the upwelling systems of the equatorial  
770 Atlantic and tropical Angola, vertical mixing is the main driver of nitrate input to the mixed layer. This  
771 is due to local mechanisms that occur in these areas (local forcing), such as the intensification of the

772 vertical shear stress between the South Equatorial Current (SEC) and the Equatorial Undercurrent  
773 (EUC) at the equator (Jouanno., 2010, Radenac et al., 2020) and the dissipation of internal tide that  
774 interact with the continental shelf and produce turbulent mixing at the Angolan coast (Körner et al.,  
775 2023, Zeng et al., 2021, Brandt et al., 2023). In the Gabon-Congo system, we can suggest that the  
776 strong stratification induced by the discharge of the Congo River, which is the second largest river in  
777 the world, contributes to thinning the mixed layer, limiting the effect of mixing very close to the  
778 surface (Dossa et al., 2019).

779 In the euphotic layer and below, the nitrate budget is almostly dictated by physical processes, which  
780 are mainly modulated by currents that transport water of different properties. We noted that vertical  
781 and zonal advectons were the drivers of nitrate input in the upwelling period, while vertical mixing  
782 and meridional advection were the drivers of nitrate losses in the lower part of the euphotic layer (just  
783 below the mixed layer depth) in this period. However, during the downwelling period, vertical mixing  
784 mostly brings nitrate to the lower part of the euphotic layer, while vertical and meridional advection  
785 always remove nitrate. Meridional advection is therefore the main factor in nitrate loss in the euphotic  
786 layer all year long. This is consistent with the warming effect of meridional advection shown by  
787 Körner et al. (2023) in the Angolan upwelling. Radenac et al (2020) showed that in the equatorial  
788 euphotic layer, zonal advection by the EUC current was the main driver of nitrate losses, which may  
789 explain our previous results since the southward Angola current dominating the ocean circulation in  
790 the Congo-Angola zone is fed by the EUC current. Indeed, the EUC, whose source waters come from  
791 the oligotrophic layers of the subtropical South Atlantic, has relatively low nitrate concentrations  
792 compared to neighbouring waters (Schott et al., 1998; Johns et al., 2014; Tuchen et al., 2022a). These  
793 low nitrate waters are brought to the Congo-Angola system by the Angola Current (AC) (Fig.16),  
794 reducing nitrate concentration in the euphotic layer. At the same time, the AC brings CHLa into the  
795 euphotic layer by meridional advection, as the EUC has relatively high CHLa concentrations (Radenac  
796 et al., 2020). This low nitrate / high CHLa signature of the AC can be seen in the first hundred metres  
797 and in particular at the base of the euphotic layer along the Gabon-Congo coast (Fig.A1c), where the  
798 AC flows (Kopte et al, 2017). Further analyses show that the coastal CHLa maximum occurs from  
799 May to September with a peak in August, which is consistent with the seasonal cycle of the CHLa  
800 concentration in the EUC (Radenac et al, 2020; Brandt et al, 2023). The simultaneous variation in  
801 current and gradient appears to be the main factor contributing to variations in the meridional  
802 advection and nitrate removal, mainly between July and October. Over the same period, we observe a  
803 sign change of the meridional nitrate gradient (Fig.14b), which is generally positive (indicating that  
804 under the mixed layer, waters to the south of the coastal box (0°N–6°S, 1° width from the coast; see  
805 Fig. 1b) are less nitrate-rich than waters to the north) under the mixed layer from January to June.



806

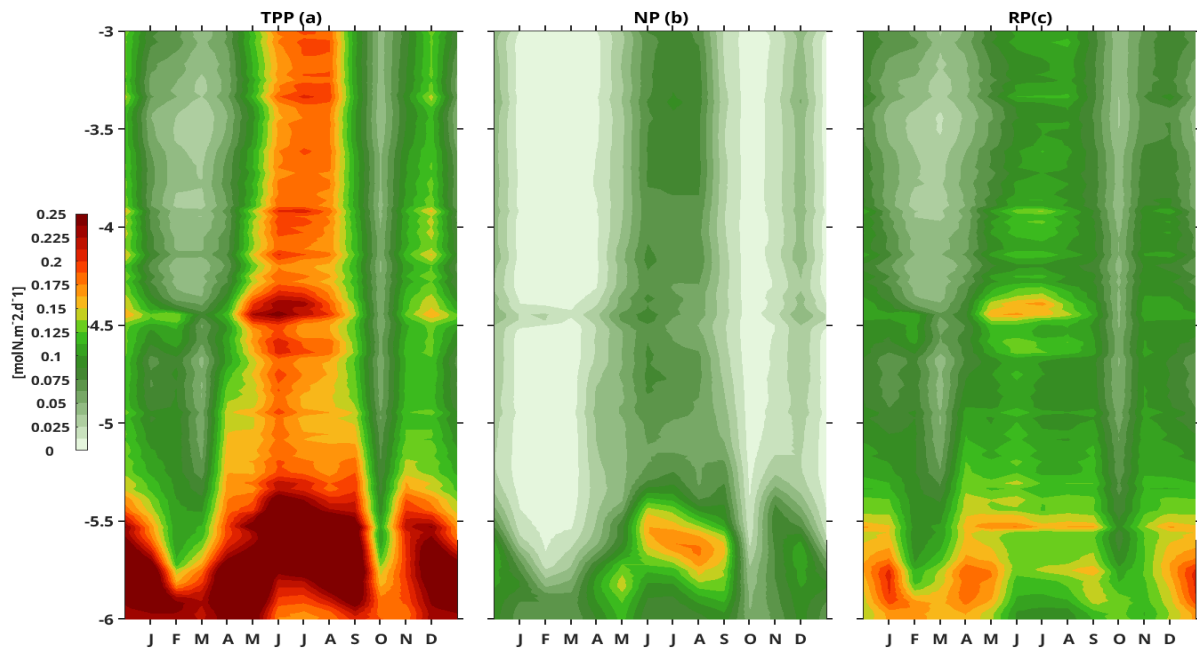
807 **Figure 16:** Regional distribution of mean annual nitrate and CHLa concentration (a, b respectively) averaged on  
 808 the 0-100 m layer along the Gabon-Congo upwelling area, black line represents different boundaries of our  
 809 Coastal box with a width of 1° of longitude relative to the coast.

810 This observation suggests that for the period from September to October, waters in the southern part of  
 811 the box are now richer in nitrate than waters in the northern part of the box under the mixed layer.  
 812 Beyond horizontal transport, this frontogenesis is also driven by the meridional gradient of vertical  
 813 motion ( $\partial w/\partial y$ ). A stronger upward vertical velocity in the southern section (near 6°S) compared to the  
 814 north leads to a higher vertical nitrate supply in the south, establishing the negative meridional nitrate  
 815 gradient observed in Fig. 14b. This highlights the important role of vertical processes in the regional  
 816 enrichment, as also emphasized by Nubi et al. (2016) for the equatorial band. This also reflects the  
 817 passage of low-nitrate waters from the EUC via the Angola Current to the Gabon-Congo coast.  
 818 However, we find that zonal advection brings nitrate in the euphotic layer and its decomposition has  
 819 shown that its variation is mostly influenced by zonal nitrate gradient variation, with a secondary  
 820 contribution of zonal current variation. This zonal current variation is seen to remove nitrate in the  
 821 euphotic layer during February-March and July-October. We can also see that in these periods the  
 822 zonal current flows toward the coast, which suggests that it brings low nitrate water from offshore  
 823 toward the coast. This seasonally eastward current is consistent with the seasonal cycle of SEUC  
 824 (Siegfried et al., 2019; Assene et al., 2022). Besides this, we can also see that there is a sign change of  
 825 the zonal nitrate gradient (Fig.13b) which occurs simultaneously with the sign change of the  
 826 meridional nitrate gradient (Fig.14b) suggesting that this inversion in zonal nitrate gradient is due to  
 827 Angola Current water at the coast. In fact, this later result highlights that the Angolan Current waters  
 828 flowing along the coast are less rich in nitrate than the water brought from offshore toward the coast by  
 829 the SEUC. As nitrate concentration in the coast is lower, SEUC waters act to increase nitrate  
 830 concentration in our coastal box, through zonal advection in the euphotic layer from April to  
 831 December. The CHLa budget analysis (Appendix A, Fig. A1) shows that the SEUC brings through  
 832 zonal advection low CHLa water at the coast thereby reducing the nitrate input during the

833 downwelling period. In the nitrate budget we saw that the main driver of nitrate input was vertical  
834 advection associated with CTWs. Körner et al. (2024) have shown, using satellite and mooring data,  
835 that CTWs detected in the SLA are of the low vertical mode, while the movement of the isopycnals is  
836 rather consistent with the vertical velocity structure of higher modes. This explains why isopycnals  
837 reach their seasonal minimum/maximum depth (in phase with the nitracline) after the minimum in  
838 SLA (Körner et al, 2024). The spatial distribution of mean annual nitrate and CHLa concentrations  
839 (Fig. 16a, b) provides clear evidence of the influence of the Angola Current (AC) on the coastal  
840 biogeochemistry of the Gabon-Congo system. Physically, the AC is a southward-flowing coastal  
841 current that advects warm, equatorial-origin waters along the shelf. Biogeochemically, our model  
842 results (Fig. 16a) show that while the broader coastal box is enriched in nutrients due to upwelling and  
843 riverine inputs, there is a distinct relative decrease in nitrate concentrations strictly along the shoreline,  
844 particularly south of 5°S. In this narrow coastal band, NO<sub>3</sub> values are lower than those found in the core  
845 of the upwelling plume located slightly further offshore. Conversely, the chlorophyll-a map (Fig. 16b)  
846 reveals a robust coastal belt with maximum concentrations exceeding 4.5 mg·m<sup>-3</sup> right at the coast.  
847 This low-nitrate / high-CHLa inverse relationship at the immediate coastline is consistent with the  
848 known characteristics of the Angola Current. Indeed, the AC transports mature waters originating from  
849 the Equatorial Undercurrent (EUC).

850 We assessed the variability of biological productivity using the PISCES component of our coupled  
851 model (Fig. 18). The results show a clear semi-annual cycle of Net Primary Production (NPP), New  
852 Production (NP), and Regenerated Production (RP), which is consistent with the seasonal cycle of  
853 nitrate and CHLa concentrations observed in the region (Körner et al., 2024). The highest values of  
854 NPP (Fig. 17a) are found near the Congo River mouth (between 5.5°S and 6°S), where average values  
855 exceed 0.20 mol N·m<sup>-2</sup>·d<sup>-1</sup>. During the main upwelling period (June–August), the NPP reaches its  
856 maximum, with local peaks near 6°S exceeding 0.25 mol N·m<sup>-2</sup>·d<sup>-1</sup>. This intensity is comparable to,  
857 though slightly lower than, the average primary production reported for the Benguela and Humboldt  
858 systems, which reach 0.37 and 0.33 mol N·m<sup>-2</sup>·d<sup>-1</sup> respectively (converted from Tilstone et al., 2009;  
859 Monteiro et al., 2010).

860 The secondary upwelling period in December also shows high productivity, with NPP values reaching  
861 approximately 0.22 mol N·m<sup>-2</sup>·d<sup>-1</sup> near the river mouth. In contrast, during the downwelling periods  
862 (notably in March and October), the system becomes less productive, with NPP dropping below  
863 0.075 mol N·m<sup>-2</sup>·d<sup>-1</sup> in most of the coastal box. The analysis of production components reveals that  
864 during the main upwelling season, the New Production (NP) (Fig. 17b) peaks at around  
865 0.15 mol N·m<sup>-2</sup>·d<sup>-1</sup>, representing about 50–60% of the NPP. In December, the NP contribution is  
866 lower, around 0.10 mol N·m<sup>-2</sup>·d<sup>-1</sup>. The Regenerated Production (RP) (Fig. 17c) remains a significant  
867 and stable driver of productivity throughout the year, particularly near the Congo mouth where it often  
868 exceeds 0.125 mol N·m<sup>-2</sup>·d<sup>-1</sup>, highlighting the importance of nutrient recycling in this river-influenced  
869 system.



871

872 **Figure 17:** Latitude-Time Hovmöller diagram of biological productivity: Net Primary Production (a), New  
 873 Production (b) and regenerated Production (c) in the coastal box (6°S-3°S, 1° wide along the coastline). The  
 874 units are milli mol per cubic meter per day.

875 High values of Net Primary Production (NPP) are also observed around 4.47°S, near the mouth of the  
 876 Kouilou River, following the characteristic semi-annual cycle of the region. A detailed comparison of  
 877 the production components (Fig. 17b, c) reveals that Regenerated Production (RP), fueled by the  
 878 recycling of nutrients within the euphotic layer, is generally higher than New Production (NP). These  
 879 two parameters remain consistent with the seasonal cycle of nitrate concentrations described  
 880 previously.

881 The seasonal cycle of NPP in the Gabon-Congo system differs from those of the ~~Namibia and~~  
 882 Benguela upwellings (*including the Namibian area*), which are primarily wind-forced systems  
 883 (Gutknecht et al., 2013). A key distinction lies in the efficiency of nitrate utilization: in our study area,  
 884 the contribution of New Production to the total NPP is notably high. For instance, while the *f-ratio*  
 885 (NP/NPP) in the Benguela system typically ranges between 0.2 and 0.4 (Monteiro et al., 2010), it  
 886 reaches approximately 0.6 in the Gabon-Congo coastal box, indicating that more than half of the  
 887 primary production is sustained by the upward supply of new nitrates.

888 Finally, we demonstrate that the conclusions regarding the nitrate budget are highly sensitive to the  
 889 definition of the Mixed Layer Depth (MLD). In this study, we adopted a 3 m reference depth for the  
 890 MLD calculation, following the criterion proposed by Aroucha et al. (2025). This shallower definition  
 891 is more appropriate for the Gabon-Congo system, as it accurately captures the intense surface  
 892 stratification induced by the river's freshwater plume. With this refined MLD criterion, our results  
 893 show a significant shift in the balance of vertical processes: vertical diffusion (mixing) now emerges  
 894 as the dominant mechanism supplying nitrate to the mixed layer, outweighing the contribution of

895 vertical advection. This finding aligns with recent observations in the Angolan upwelling (Brandt et  
896 al., 2023; Körner et al., 2023, 2024) and the Gabon-Congo plume region (Scannell and McPhaden,  
897 2018; Ngakala et al., 2025), which highlight turbulent mixing—often fueled by internal tides and  
898 shear—as a major driver of vertical nutrient and heat fluxes. This shift emphasizes the critical role of  
899 the 'Barrier Layer' and the strong surface halocline in trapping nutrients and modulating their upward  
900 transfer through small-scale mixing processes rather than mean vertical motion.

## 901 **5 Conclusion**

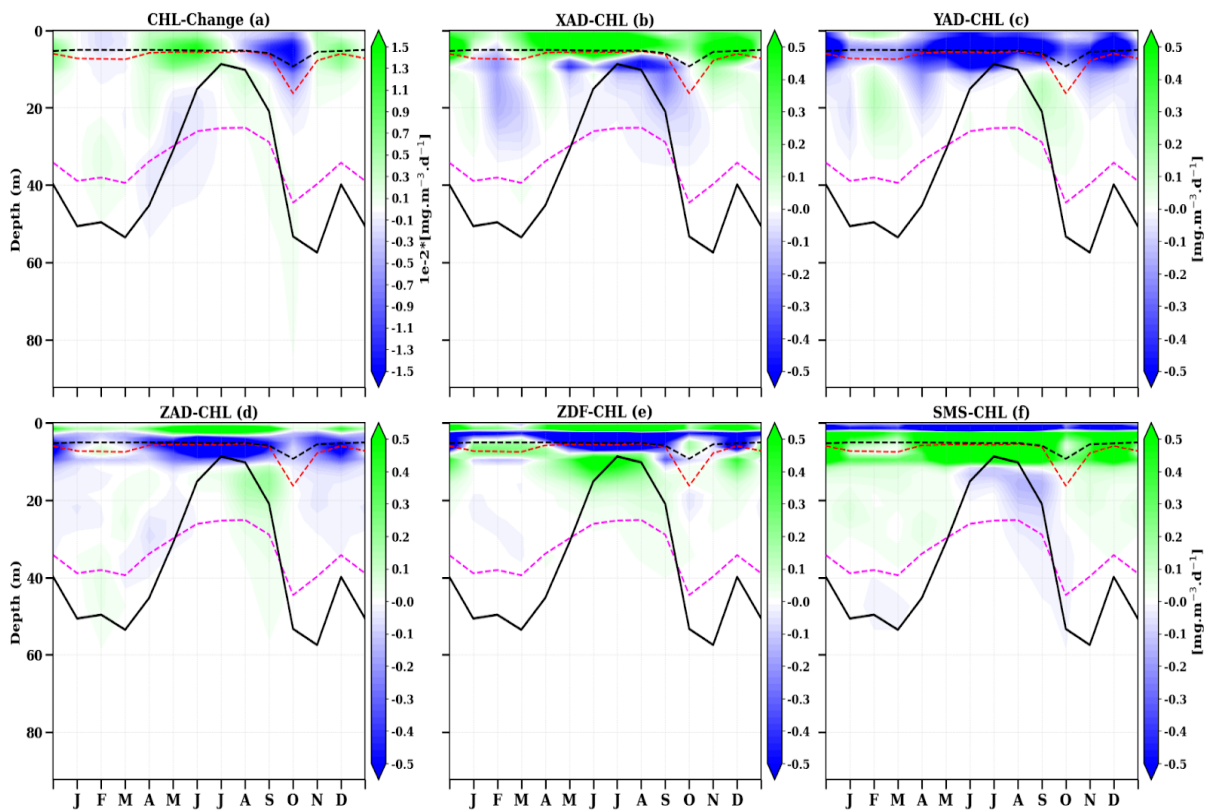
902 Throughout this work we have described and analysed the seasonal cycles in nitrate and CHLa  
903 concentrations, as well as the physical and biological processes that modulate nitrate supply and  
904 biological productivity in the mixed layer and in the euphotic layer in the Gabon-Congo upwelling  
905 system. We began by validating a regional high-resolution ( $1/36^\circ$ ) simulation of the coupled  
906 physical-biogeochemical model NEMO-PISCES in this area for the studied year 2011. Surface and  
907 subsurface validation of the simulation using observations (satellite, in situ, climatology) shows that  
908 the model reasonably reproduces the main physical and biogeochemical characteristics of the study  
909 area. Subsequently, the seasonal cycle of nitrate shows that there are two periods of upwelling and two  
910 periods of downwelling (Fig. 4e,f and Fig. 11a). These upwelling and downwelling are associated with  
911 remote forcing : Kelvin waves that propagate along the equator and the coastal waveguide force the  
912 vertical migrations of the thermocline, which is also a proxy for the nitracline. The seasonal cycle of  
913 CHLa is explained by that of nitrate. The assessment of the nitrate balance in the mixed layer shows  
914 that the main nitrate is mainly supplied in the mixed layer by vertical diffusion (Fig. 10f), vertical  
915 advection (Fig. 10d) and zonal advection (Fig. 10c), which is mainly modulated by nitrate inputs from  
916 the Congo River at  $6^\circ\text{S}$ . The vertical advection induced by CTWs and vertical diffusion play also a  
917 role in the nitrate supply, while nitrate losses are linked to meridional advection and the biological  
918 activity (photosynthesis). In the lower part of the euphotic layer, on the other hand, nitrate is supplied  
919 by zonal advection and vertical advection. Vertical diffusion contributes to nitrate losses, except in  
920 downwelling periods where it represents one of the main drivers of nitrate supply. We have also seen  
921 that meridional advection via the Angola Current, which transports the low-nitrate warm waters of the  
922 Equatorial undercurrent, is the main driver of nitrate loss below the mixed layer throughout the year.  
923 We find that vertical advection is controlled by the vertical nitrate gradient and nitrate input (Fig. 15),  
924 rather than vertical velocity, when it brings nitrate into the mixed layer during the main upwelling  
925 period. However, in the secondary upwelling in December, vertical advection also brings nitrate, but is  
926 then mostly controlled by vertical velocity.

927 In future works, the interannual variability will be studied, specifically in association with the  
928 interannual variability of the Congo River discharges. ~~In future works, the interannual variability will~~  
929 ~~be study especially associated with the interannual variability of the Congo river discharges~~ (Scannell  
930 and McPhaden (2018), Körner et al., 2023, 2024; Brandt et al., 2023) and of the CTWs forced by the  
931 Equatorial Kelvin waves (e.g. Bachèlery et al., 2015, 2016). Understanding the seasonal and

932 interannual variability of productivity is of primary interest to ensure the sustainability of ecosystems  
 933 and fisheries in the Gabon-Congo upwelling system.

### 934 Appendix A : Euphotic Layer CHLa Budget Analysis

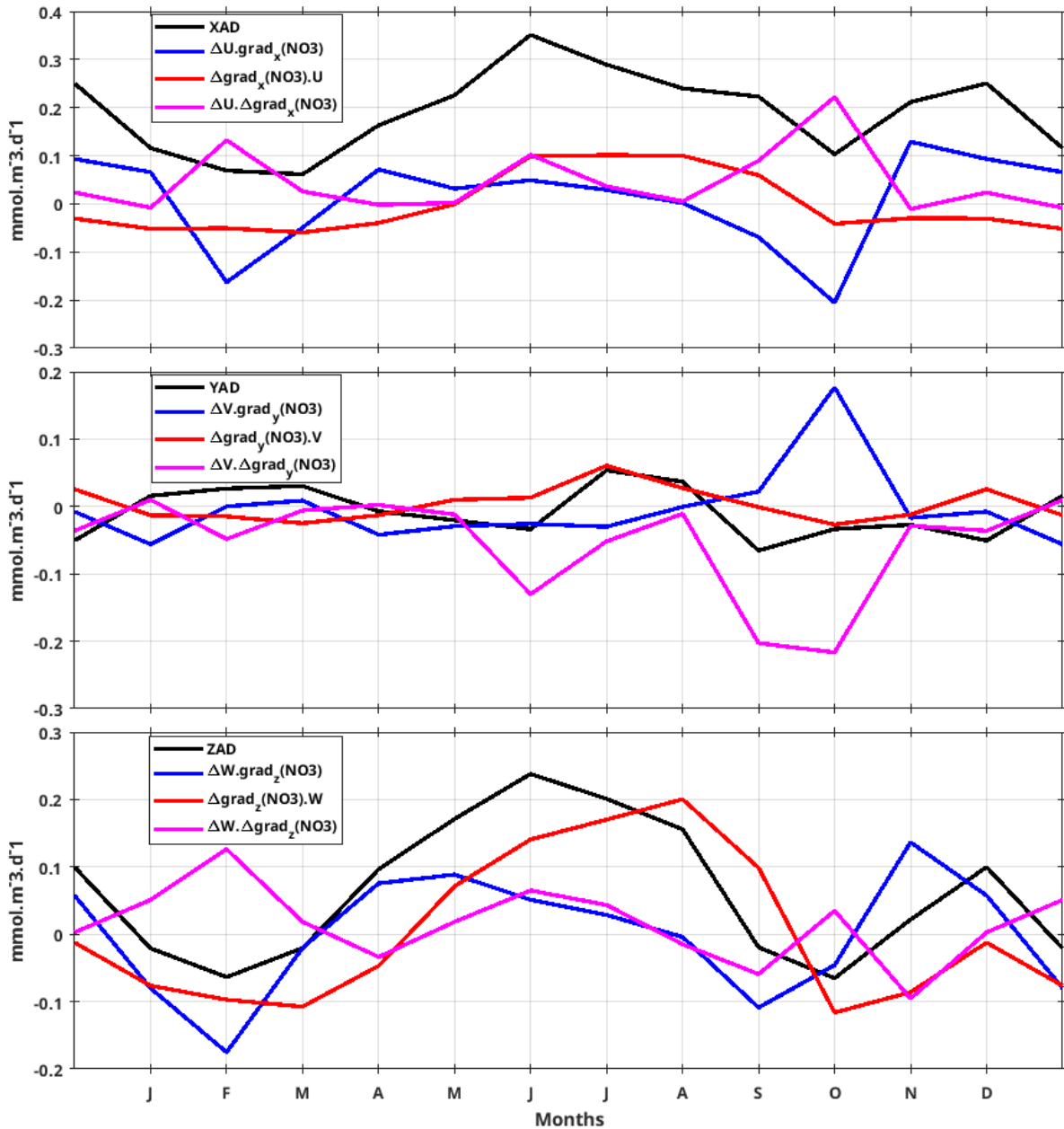
935 In the lower part of the euphotic zone, the CHLa budget (Fig. A1) is primarily governed by the  
 936 interaction between coastal and offshore water masses. During the downwelling period, the zonal  
 937 advection term (XAD\_CHL) shows a net loss of CHLa near the base of the euphotic layer. This is  
 938 explained by the passage of the South Equatorial Undercurrent (SEUC). As described by Nubi et al.  
 939 (2016), undercurrent waters (EUC/SEUC) are relatively nitrate-poor and carry less CHLa than the  
 940 highly productive coastal waters. The eastward transport of these offshore waters towards the  
 941 Gabon-Congo coast leads to a dilution of the local CHLa concentration, a process captured by the  
 942 negative values in the zonal advection budget.



943 **Figure A1:** Depth-time Hovmöller diagram of the seasonal chlorophyll-a budget along the Gabon-Congo coast  
 944 (6°S–0°N, 1° coastal strip) for: (a) total rate of change (CHL-change), (b) zonal advection (XAD-CHL), (c)  
 945 meridional advection (YAD-CHL), (d) vertical advection (ZAD-CHL), (e) vertical diffusion (ZDF-CHL), and (f)  
 946 biological source-minus-sink term (SMS-CHL). Units for all panels are  $\text{mg m}^{-3} \text{d}^{-1}$ . The black solid line  
 947 represents the thermocline (20°C isotherm), while dashed magenta, red and black lines indicate the euphotic,  
 948 isothermal and mixed layer depths, respectively.

### 950 Appendix B : Euphotic Layer Nitrate Advections Components Analysis

951 To further investigate this relationship, the individual contributions of seasonal current and  
 952 gradient variations are shown in **Appendix B (Fig. B1)**. This decomposition confirms that the  
 953 mean flow acting on seasonal gradient anomalies is the dominant driver of advection variability.



954

955 **Figure B1:** Seasonal variation of advection components averaged in the euphotic layer, black line represent  
 956 zonal, meridional and vertical advection in (a), (b) and (c) respectively. The red line in both three figures  
 957 represents gradient variation, blue line is current variation and magenta line represents the simultaneous  
 958 variation of gradient and current.

959 **Code and data availability.** Publicly available datasets were used for this study. Chlorophyll data  
 960 (1998–2020) are from the Copernicus-GlobColour dataset (<https://doi.org/10.48670/moi-00281>,  
 961 Copernicus, 2023a). The sea level anomaly data (1998–2020) were accessed via the Copernicus Server  
 962 (<https://doi.org/10.48670/moi-00148>, Copernicus, 2023b). The MUR SST product created by the JPL

963 MUR MEaSURES program as part of the GHRSSST (Group for High-Resolution Sea Surface  
964 Temperature) project is obtained from <https://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1>  
965 (Chin et al., 2017) and ASCAT wind data <https://podaac.jpl.nasa.gov/dataset/ASCATB-L2-25km>. The  
966 nutrient fields were assessed using the CSIRO Atlas of Regional Seas climatology (Dunn and  
967 Ridgway, 2002) ,  
968 <https://portal.aodn.org.au/search?uuid=d9302a48-57b1-41c2-a0dc-78bd00dd5e4b>[https://thredds.aodn-](https://thredds.aodn.org.au/thredds/catalog/CSIRO/Climatology/CARS/2009/AODN-product/catalog.html?dataset=CSIRO/Climatology/CARS/2009/AODN-product/)  
969 [org.au/thredds/catalog/CSIRO/Climatology/CARS/2009/AODN-product/catalog.html?dataset=CSIRO](https://thredds.aodn.org.au/thredds/catalog/CSIRO/Climatology/CARS/2009/AODN-product/catalog.html?dataset=CSIRO/Climatology/CARS/2009/AODN-product/)  
970 [/Climatology/CARS/2009/AODN-product/](https://thredds.aodn.org.au/thredds/catalog/CSIRO/Climatology/CARS/2009/AODN-product/catalog.html?dataset=CSIRO/Climatology/CARS/2009/AODN-product/). Near surface currents from the Ocean Surface Current  
971 Analysis Real-time (OSCAR, Johnson et al. 2007),  
972 [https://podaac.jpl.nasa.gov/dataset/OSCAR\\_L4\\_OC\\_INTERIM\\_V2.0](https://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_INTERIM_V2.0). Model outputs are available  
973 from the authors, especially GA, ID, GM, and JJ.

974

975 **Author contributions.** LJME outlined and wrote the paper. LJME and RDG produced the figures.  
976 GM has run the NEMO-PISCES model. GA, ID, CYD the co-authors contributed to define  
977 methodology and reviewed the paper.

978 **Conflict of Interest.** The authors declare that they have no conflict of interest.

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985 [car/oscar-surface-currents/](https://www.csr.org/research/oscar/oscar-surface-currents/)) to provide OSCAR current data.

986 Also thanks to  
987 <https://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1><https://podaac.jpl.nasa.gov/> for providing  
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## 991 **References**

992 ~~Assene, F., Morel, Y., Delpech, A., Aguedjou, M., Jouanno, J., Cravatte, S., Marin, F., Ménesguen, C.,~~  
993 ~~Chaigneau, A., Dadou, I., Alory, G., Holmes, R., Bourlès, B., & Koch-larrouy, A. (2020). From~~  
994 ~~Mixing to the Large Scale Circulation : How the Inverse Cascade Is Involved in the Formation of the~~  
995 ~~Subsurface Currents in the Gulf of Guinea. 1-36. <https://doi.org/10.3390/fluids5030147>. ¶~~

996 Aumont, O. and Bopp, L.: Globalizing results from ocean insitu iron fertilization experiments, *Global*  
997 *Biogeochem. Cy.*, 20, GB2017, <https://doi.org/10.1029/2005GB002591>, 2006.¶

998 Aumont, O., Belviso, S., and Monfray, P.: Dimethylsulfide (DMS) cycle with a 3-D  
999 ocean biogeochemical model, *Oceanogr. Lit. Rev.*, 11, 1637, <https://doi.org/10.1029/98GB02757>,  
1000 1998.¶

1001 Aumont, O., Ethé, C., Tagliabue, A., Bopp, L., and Gehlen, M.: PISCES-v2: an ocean biogeochemical  
1002 model for carbon and ecosystem studies, *Geosci. Model Dev.*, 8, 2465–2513,  
1003 <https://doi.org/10.5194/gmd-8-2465-2015>, 2015.¶

1004 Awo, F. M., Alory, G., Da-Allada, C. Y., Delcroix, T., Jouanno, J., Kestenare, E., and Baloïtcha, E.: On  
1005 the seasonal and interannual variability of the sea surface salinity in the Gulf of Guinea, *Clim. Dynam.*,  
1006 60, 2121–2140, <https://doi.org/10.1007/s00382-022-06443-4>, 2023.¶

1007 Awo, F. M., Rouault, M., Ostrowski, M., Tomety, F. S., Da-Allada, C. Y., and Jouanno, J.: Seasonal  
1008 cycle of sea surface salinity in the Angola Upwelling System, *J. Geophys. Res. Oceans*, 127,  
1009 e2022JC018518, <https://doi.org/10.1029/2022JC018518>, 2022.¶

1010 Bachèlery, M. L. (2016). Variabilité côtière physique et biogéochimique en Atlantique Sud-Est: rôle du  
1011 forçage atmosphérique local versus téléconnexion océanique (Doctoral dissertation, Ph. D. thesis,  
1012 Toulouse: Laboratoire d'Etude en Géophysique et Océanographie Spatiale (LEGOS), University of  
1013 Paul Sabatier, 215).¶

1014 Bachèlery, M. L., Illig, S., and Dadou, I.: Interannual variability in the South-East Atlantic Ocean,  
1015 focusing on the Benguela Upwelling System: Remote versus local forcing, *J. Geophys. Res. Oceans*,  
1016 121, 284–310, <https://doi.org/10.1002/2015JC011168>, 2015.¶

1017 Bourlès, B., Molinari, R. L., Johns, W. E., Gouriou, Y., and Carder, K. L.: The South Equatorial  
1018 Undercurrent in the Atlantic Ocean, *Geophys. Res. Lett.*, 31, L14301,  
1019 <https://doi.org/10.1029/2004GL020020>, 2004.¶

1020 Brandt, P., Alory, G., Awo, F. M., Dengler, M., Djakouré, S., Imbol Koungue, R. A., Jouanno, J.,  
1021 Körner, M., Roch, M., and Rouault, M. (2023). Physical processes and biological productivity in the  
1022 upwelling regions of the tropical Atlantic. *Ocean Science*, 19(3):581–601,  
1023 <https://doi.org/10.5194/os-19-581-2023>¶

1024 Cabos, W., Sein, D. V., Pinto, J. G., Koseki, S., Álvarez-García, F. J., & Durán-Quesada, A. M. (2017).  
1025 The coastal upwelling system of the southeast Atlantic as simulated by a high resolution coupled  
1026 model. *Climate Dynamics*, 49(5), 1809–1828. <https://doi.org/10.1007/s00382-016-3319-9>¶

1027 Caniaux, G., Giordani, H., Redelsperger, J. L., Guichard, F., Key, E., and Wade, M.: Coupling between  
1028 the Atlantic cold tongue and the West African monsoon in boreal spring and summer, *J. Geophys.*  
1029 *Res. Oceans*, 116, C04003, <https://doi.org/10.1029/2010jc006570>, 2011.¶

1030 Carr, M. E. (2002). Estimation of potential productivity in Eastern Boundary Currents using remote  
1031 sensing. *Deep Sea Research Part II: Topical Studies in Oceanography*, 49(1-3):59-80.¶

1032 Chavez, F. P., & Messié, M. (2009). A comparison of eastern boundary upwelling ecosystems.  
1033 *Progress in Oceanography*, 83(1-4), 80-96.¶

1034 Chin, T.M, J Vazquez-Cuervo et E Armstrong (2017). "A multi-scale high-resolution analysis of global  
1035 sea surface temperature". In : *Remote sensing of environment 200*, p. 154-169.¶

1036 de Boyer Montégut, C., Madec, G., Fischer, A. S., Lazar, A., and Iudicone, D.: Mixed layer depth over  
1037 the global ocean: An examination of profile data and a profile-based climatology, *J. Geophys. Res.*  
1038 *Oceans*, 109, C12003, <https://doi.org/10.1029/2004JC002378>, 2004.¶

1039 Dorothee Bonhoure, Elizabeth Rowe, Arthur J. Mariano, Edward H. Ryan. "The South Equatorial Sys-  
1040 Current." *Ocean Surface Currents*.(2004).¶

1041 <https://oceancurrents.rsmas.miami.edu/atlantic/south-equatorial.html>¶

1042 Dossa, A., Da Allada, C., Herbert, G., & Bourlès, B. (2019). Seasonal cycle of the salinity barrier layer  
1043 revealed in the northeastern Gulf of Guinea. *African Journal of Marine Science*, 41(2), 163-175.  
1044 <https://doi.org/10.2989/1814232X.2019.1616612>¶

1045 Ducet, N., Le Traon, P. Y., & Reverdun, G. (2000). Global high-resolution mapping of ocean  
1046 circulation from TOPEX/Poseidon and ERS-1 and -2. *Journal of Geophysical Research*, 105(C819),  
1047 19477-19498. <https://doi.org/10.1029/2000jc900063>¶

1048 Dunn, J. R. and Ridgway, K. R.: Mapping ocean properties in regions of complex topography, *Deep*  
1049 *Sea Res. Part I*, 49, 591-604, [https://doi.org/10.1016/S0967-0637\(01\)00069-3](https://doi.org/10.1016/S0967-0637(01)00069-3), 2002.¶

1050 Estival, R., Quiniou, V., Messenger, C., 2013. Real-time network of weather and ocean stations:  
1051 public-private partnership on in-situ measurements in the Gulf of Guinea. *Sea Technol.* 54 (3), 34-38.¶

1052 FAO: Fishery and Aquaculture Country Profiles, Angola, 2020, Country Profile Fact Sheets, Fisheries  
1053 and Aquaculture Division [online], Rome, <https://www.fao.org/fishery/en/facp/ago?lang=en> (last  
1054 access: 11 April 2023), updated 7 February 2022.¶

1055 Fréon, P., Barange, M., & Aristegui, J. (2009). Eastern boundary upwelling ecosystems: integrative  
1056 and comparative approaches. *Progress in Oceanography*, 83(1-4), 1-14.¶

1057 Gutknecht, E., Dadou, I., Marchesiello, P., Cambon, G., Le Vu, B., Sudre, J., Garçon, V., Machu, E.,  
1058 Rixen, T., Kock, A., Flohr, A., Paulmier, A., and Lavik, G. (2013). Nitrogen transfers off Walvis Bay:  
1059 a 3-D coupled physical/biogeochemical modeling approach in the Namibian upwelling system.  
1060 *Biogeosciences*, 10(6):4117-4135.¶

1061 ~~Hardman-Mountford, N. J. and McGlade, J. S.: Retrieval of phytoplankton biomass from ocean colour~~  
1062 ~~in the Benguela ecosystem, *Remote Sens. Environ.*, 79, 11–23,~~  
1063 ~~[https://doi.org/10.1016/S0034-4257\(01\)00236-0](https://doi.org/10.1016/S0034-4257(01)00236-0), 2002.¶~~

1064 ~~Hopkins, J., Lucas, M., Dufau, C., Sutton, M., Stum, J., Lauret, O., & Channelliere, C. (2013).~~  
1065 ~~Detection and variability of the Congo River plume from satellite derived sea surface temperature,~~  
1066 ~~salinity, ocean colour and sea level. *Remote Sensing of Environment*, 139, 365–385.~~  
1067 ~~<https://doi.org/10.1016/j.rse.2013.08.015>¶~~

1068 ~~Hutchings, L., van der Lingen, C. D., Shannon, L. J., Crawford, R. J. M., Verheye, H. M. S.,~~  
1069 ~~Bartholomae, C. H., van der Plas, A. K., Louw, D., Kreiner, A., Ostrowski, M., Fidel, Q., Barlow, R.~~  
1070 ~~G., Lamont, T., Coetzee, J., Shillington, F., Veitch, J., Currie, J. C., and Monteiro, P. M. S.: The~~  
1071 ~~Benguela Current: An ecosystem of four components, *Prog. Oceanogr.*, 83, 15–32,~~  
1072 ~~<https://doi.org/10.1016/j.pocean.2009.07.046>, 2009.¶~~

1073 ~~Johns, W. E., Brandt, P., Lumpkin, R., Fischer, J., Hormann, V., Pirani, A., Schmid, C., and Bourlès,~~  
1074 ~~B.: Variation of upper ocean seasonal and interannual velocity structure in the eastern equatorial~~  
1075 ~~Atlantic, *J. Phys. Oceanogr.*, 44, 1201–1212, <https://doi.org/10.1175/JPO-D-13-0132.1>, 2014.¶~~

1076 ~~Johnson, E. S., Bonjean, F., Lagerloef, G. S., Gunn, J. T., & Mitchum, G. T. (2007). Validation and~~  
1077 ~~error analysis of OSCAR sea surface currents. *Journal of Atmospheric and Oceanic Technology*, 24(4),~~  
1078 ~~688–701.¶~~

1079 ~~Jouanno, J.: Influence de la dynamique de l'Atlantique équatorial sur la variabilité de la langue froide,~~  
1080 ~~*PhD thesis*, Université de Toulouse III, <http://thesesups.ups-tlse.fr/1154/>, 2010.¶~~

1081 ~~Kobayashi, S., Ota, Y., Harada, Y., Ebata, A., Moriya, M., Onoda, H., Onogi, K., Kamiguchi, H.,~~  
1082 ~~Kobayashi, C., Endo, H., Miyaoka, K., and Takahashi, K.: The JRA-55 Reanalysis: General~~  
1083 ~~specifications and basic characteristics, *J. Meteorol. Soc. Jpn.*, 93, 5–48,~~  
1084 ~~<https://doi.org/10.2151/jmsj.2015-001>, 2015.¶~~

1085 ~~Kopte, R. (2017). The Angola Current in a Tropical Seasonal Upwelling System: Seasonal Variability~~  
1086 ~~in Response to Remote Equatorial and Local Forcing (Doctoral dissertation, Christian Albrechts~~  
1087 ~~Universität Kiel).¶~~

1088 ~~Körner, M., Brandt, P., and Dengler, M.: Seasonal cycle of sea surface temperature in the tropical~~  
1089 ~~Angolan Upwelling System, *Ocean Sci.*, 19, 121–139, <https://doi.org/10.5194/os-19-121-2023>, 2023.¶~~

1090 ~~Körner, M., Brandt, P., and Dengler, M.: Seasonal cycle of sea surface temperature in the tropical~~  
1091 ~~Angolan upwelling system, *Ocean Sci.*, 19, 121–139, <https://doi.org/10.5194/os-19-121-2023>, 2023.¶~~

1092 ~~Körner, M., Brandt, P., Illig, S., Dengler, M., Subramaniam, A., Bachèlery, M. Lou, and Krahnmann, G.:~~  
1093 ~~Coastal trapped waves and tidal mixing control primary production in the tropical Angolan upwelling~~  
1094 ~~system, *Sci. Adv.*, 10, 29–31, <https://doi.org/10.1126/sciadv.adj6686>, 2024.¶~~

1095 Locarnini, M. M., Mishonov, A. V., Baranova, O. K., Boyer, T. P., Zweng, M. M., Garcia, H. E., ... &  
1096 Smolyar, I. (2018). World ocean atlas 2018, volume 1: Temperature.¶

1097 Koseki, S., Cabos, W., Sein, D. V., & Mohino, E. (2018). The role of the Gulf of Guinea upwelling in  
1098 the atmospheric circulation of the tropical Atlantic in a high-resolution coupled model. *Climate*  
1099 *Dynamics*, 51(3), 1017–1035. <https://doi.org/10.1007/s00382-017-3896-2>¶

1100 Koubanova, M., Koseki, S., & Keenlyside, N. S. (2018). Seasonal variability of the Atlantic cold  
1101 tongue and its relationship with the Angola-Benguela upwelling system. *Climate Dynamics*, 51(7),  
1102 2975–2993. <https://doi.org/10.1007/s00382-018-4197-0>¶

1103 Loukos, H. and Mémerly, L.: Simulation of the nitrate seasonal cycle in the equatorial Atlantic ocean  
1104 during 1983 and 1984, *J. Geophys. Res.*, 104, 15549–15573, 1999.¶

1105 Madec, G. and the NEMO System Team, 2024. *NEMO Ocean Engine Reference Manual*, Zenodo.  
1106 <https://doi.org/10.5281/zenodo.1464816>¶

1107 Messié, M., & Chavez, F. P. (2015). Seasonal regulation of primary production in eastern boundary  
1108 upwelling systems. *Progress in Oceanography*, 134, 1-18.¶

1109 Monteiro, P., Dewitte, B., Scranton, M., Paulmier, A., and Van der Plas, A. (2011). The role of open  
1110 ocean boundary forcing on seasonal to decadal scale variability and long term change of natural shelf  
1111 hypoxia. *Environmental Research Letters*, (6):1–14.¶

1112 Ngakala, R. D., Alory, G., Da Allada, C. Y., Dadou, I., Cardot, C., Morvan, G., ... & Baloitcha, E.  
1113 (2025). Seasonal mixed layer temperature in the Congolese upwelling system. *Journal of Geophysical*  
1114 *Research: Oceans*, 130(1), e2023JC020528.¶

1115 Nieto, K., & Mélin, F. (2017). Variability of chlorophyll a concentration in the Gulf of Guinea and its  
1116 relation to physical oceanographic variables. *Progress in oceanography*, 151, 97–115.¶

1117 Nubi, O., Bourles, B., & Edokpayi, C. (2016). On the Nutrient distribution and phytoplankton biomass  
1118 in the Gulf of Guinea equatorial band as inferred from In-situ measurements. *Journal of*  
1119 *Oceanography and Marine Science*, 7(1), 1-11.¶

1120 Ostrowski, M., da Silva, J. C. B., and Bazik-Sangolay, B.: The response of sound scatterers to El Niño-  
1121 and La Niña-like oceanographic regimes in the southeastern Atlantic, *ICES J. Mar. Sci.*, 66,  
1122 1063–1072, <https://doi.org/10.1093/icesjms/fsp102>, 2009.¶

1123 Radenac, M. H., Jouanno, J., Tchamabi, C. C., Awo, M., Bourlès, B., Arnault, S., and Aumont, O.:  
1124 Physical drivers of the nitrate seasonal variability in the Atlantic cold tongue, *Biogeosciences*, 17,  
1125 529–545, <https://doi.org/10.5194/bg-17-529-2020>, 2020.¶

1126 Resplandy, L., Hogikyan, A., Müller, J. D., Najjar, R. G., Bange, H. W., Bianchi, D., ... & Regnier, P.  
1127 (2024). A synthesis of global coastal ocean greenhouse gas fluxes. *Global Biogeochemical Cycles*,  
1128 38(1), e2023GB007803. <https://doi.org/10.1029/2023GB007803>. [↗](#)

1129 Ridgway, K. R., J. R. Dunn, and J. L. Wilkin (2002), Ocean interpolation by four dimensional least  
1130 squares—Application to the waters around Australia, *J. Atmos. Oceanic Technol.*, 19, 1357–1375. [↗](#)

1131 Rouault, M.: Bi-annual intrusion of tropical water in the northern Benguela upwelling, *Geophys. Res.*  
1132 *Let.*, 39, L12606, <https://doi.org/10.1029/2012gl052099>, 2012. [↗](#)

1133 Scannell, H. A. and McPhaden, M. J.: Seasonal mixed layer temperature balance in the southeastern  
1134 tropical Atlantic, *J. Geophys. Res. Oceans*, 123, 5557–5570, <https://doi.org/10.1029/2018JC014099>,  
1135 2018. [↗](#)

1136 Schott, F. A., Fischer, J., and Stramma, L.: Transports and pathways of the upper layer circulation in  
1137 the western tropical Atlantic, *J. Phys. Oceanogr.*, 28, 1904–1928, [https://doi.org/10.1175/1520-](https://doi.org/10.1175/1520-0485(1998)028<1904:TAPOTU>2.0.CO;2)  
1138 [0485\(1998\)028<1904:TAPOTU>2.0.CO;2](https://doi.org/10.1175/1520-0485(1998)028<1904:TAPOTU>2.0.CO;2), 1998. [↗](#)

1139 Siegfried, L., Schmidt, M., Mohrholz, V., Pogrzeba, H., Nardini, P., Böttinger, M., and Scheuermann,  
1140 G.: The tropical-subtropical coupling in the Southeast Atlantic from the perspective of the northern  
1141 Benguela upwelling system, *Plos One*, 14, e0210083, <https://doi.org/10.1371/journal.pone.0210083>,  
1142 2019. [↗](#)

1143 Sikhakolli, R., Sharma, R., Basu, S., Gohil, B. S., Sarkar, A., & Prasad, K. V. S. R. (2013). Evaluation  
1144 of OSCAR ocean surface current product in the tropical Indian Ocean using in situ data. *Journal of*  
1145 *earth system science*, 122(1), 187–199. [↗](#)

1146 Sowman, M. and Cardoso, P.: Small-scale fisheries and food security strategies in countries in the  
1147 Benguela Current Large Marine Ecosystem (BCLME) region: Angola, Namibia and South Africa,  
1148 *Mar. Policy*, 34, 1163–1170, <https://doi.org/10.1016/j.marpol.2010.03.016>, 2010. [↗](#)

1149 Tchupalanga, P., Dengler, M., Brandt, P., Kopte, R., Macueria, M., Coelho, P., Ostrowski, M., and  
1150 Keenlyside, N. S.: Eastern Boundary Circulation and Hydrography Off Angola: Building Angolan  
1151 Oceanographic Capacities, *B. Am. Meteorol. Soc.*, 99, 1589–1605,  
1152 <https://doi.org/10.1175/Bams-D-17-0197.1>, 2018a. [↗](#)

1153 Thiam, A., Alory, G., Jouanno, J., Da Allada, C. Y., and Morvan, G.: Coastal upwelling in the  
1154 Northern Gulf of Guinea: Seasonal cycle and mesoscale interactions, *Ocean Modelling*, 188, 102300,  
1155 <https://doi.org/10.1016/j.ocemod.2024.102300>, 2024. [↗](#)

1156 Tilstone, G., Smyth, T., Poulton, A., and Hutson, R. (2009). Measured and remotely sensed estimates  
1157 of primary production in the Atlantic Ocean from 1998 to 2005. *Deep Sea Research Part II: Topical*  
1158 *Studies in Oceanography*, 56(15):918–930. [↗](#)

1159 Topé, G. D. A., Alory, G., Djakouré, S., Da-Allada, C. Y., Jouanno, J., & Morvan, G. (2023). How  
1160 does the Niger River warm coastal waters in the Northern Gulf of Guinea? *Frontiers in Marine*  
1161 *Science*, 10, 1187202. <https://doi.org/10.3389/fmars.2023.1187202>.¶

1162 Tuchen, F. P., Brandt, P., Lübbecke, J. F., and Hummels, R.: Transports and pathways of the tropical  
1163 AMOC return flow from Argo data and shipboard velocity measurements, *J. Geophys. Res.-Oceans*,  
1164 127, e2021JC018115, <https://doi.org/10.1029/2021JC018115>, 2022a.¶

1165 Voldoire, A., Belamari, S., & Lévy, M. (2019). On the role of ocean-atmosphere interaction in the  
1166 onset of the Atlantic cold tongue. *Climate Dynamics*, 53(9), 5437–5455.  
1167 <https://doi.org/10.1007/s00382-019-04717-0>¶

1168 Xu, Z., M. Li, C. M. Patricola, and P. Chang, 2014: Oceanic origin of southeast tropical Atlantic  
1169 biases. *Climate Dyn.*, 43, 2915–2930, <https://doi.org/10.1007/s00382-013-1901-y>.¶

1170 Zeng, Z., Brandt, P., Lamb, K. G., Greatbatch, R. J., Dengler, M., Claus, M., and Chen, X.:  
1171 Three-dimensional numerical simulations of internal tides in the Angolan upwelling region, *J.*  
1172 *Geophys. Res.-Oceans*, 126, e2020JC016460, <https://doi.org/10.1029/2020JC016460>, 2021.¶

1173 Zuidema, P., Redemann, J., Haywood, J., Wood, R., Piketh, S., Hipondoka, M., & Formenti, P. (2016).  
1174 Smoke and clouds above the southeast Atlantic: Upcoming field campaigns probe absorbing aerosol's  
1175 impact on climate. *Bulletin of the American Meteorological Society*, 97(7), 1131–1135.¶

1176 Zweng, M. M., Seidov, D., Boyer, T. P., Locarnini, M., Garcia, H. E., Mishonov, A. V., ... & Smolyar,  
1177 I. (2019). *World ocean atlas 2018, volume 2: Salinity*.

1178 Assene, F., Morel, Y., Delpech, A., Aguedjou, M., Jouanno, J., Cravatte, S., Marin, F., Ménesguen, C.,  
1179 Chaigneau, A., Dadou, I., Alory, G., Holmes, R., Bourlès, B., and Koch-larrouy, A.: From Mixing to  
1180 the Large Scale Circulation: How the Inverse Cascade Is Involved in the Formation of the Subsurface  
1181 Currents in the Gulf of Guinea, *Fluids*, 5, 147, <https://doi.org/10.3390/fluids5030147>, 2020.

1182 Aumont, O. and Bopp, L.: Globalizing results from ocean insitu iron fertilization experiments, *Global*  
1183 *Biogeochem. Cy.*, 20, GB2017, <https://doi.org/10.1029/2005GB002591>, 2006.

1184 Aumont, O., Belviso, S., and Monfray, P.: Dimethylsulfide (DMS) cycle with a 3-D  
1185 ocean-biogeochemical model, *Oceanogr. Lit. Rev.*, 11, 1637, <https://doi.org/10.1029/98GB02757>,  
1186 1998.

1187 Aumont, O., Ethé, C., Tagliabue, A., Bopp, L., and Gehlen, M.: PISCES-v2: an ocean biogeochemical  
1188 model for carbon and ecosystem studies, *Geosci. Model Dev.*, 8, 2465–2513,  
1189 <https://doi.org/10.5194/gmd-8-2465-2015>, 2015.

1190 Awo, F. M., Alory, G., Da-Allada, C. Y., Delcroix, T., Jouanno, J., Kestenare, E., and Baloitcha, E.: On  
1191 the seasonal and interannual variability of the sea surface salinity in the Gulf of Guinea, *Clim.*  
1192 *Dynam.*, 60, 2121–2140, <https://doi.org/10.1007/s00382-022-06443-4>, 2023.

- 1193 Awo, F. M., Rouault, M., Ostrowski, M., Tomety, F. S., Da-Allada, C. Y., and Jouanno, J.: Seasonal  
1194 cycle of sea surface salinity in the Angola Upwelling System, *J. Geophys. Res. Oceans*, 127,  
1195 e2022JC018518, <https://doi.org/10.1029/2022JC018518>, 2022.
- 1196 Bachèlery, M. L.: Variabilité côtière physique et biogéochimique en Atlantique Sud-Est: rôle du  
1197 forçage atmosphérique local versus téléconnexion océanique, PhD thesis, University of Paul Sabatier,  
1198 Toulouse, France, 215 pp., 2016.
- 1199 Bachèlery, M.-L., Illig, S., and Dadou, I.: Interannual variability in the South-East Atlantic Ocean,  
1200 focusing on the Benguela Upwelling System: Remote versus local forcing, *J. Geophys. Res. Oceans*,  
1201 121, 284–310, <https://doi.org/10.1002/2015JC011168>, 2015.
- 1202 Bourlès, B., Molinari, R. L., Johns, W. E., Gouriou, Y., and Carder, K. L.: The South Equatorial  
1203 Undercurrent in the Atlantic Ocean, *Geophys. Res. Lett.*, 31, L14301,  
1204 <https://doi.org/10.1029/2004GL020020>, 2004.
- 1205 Brandt, P., Alory, G., Awo, F. M., Dengler, M., Djakouré, S., Imbol Koungue, R. A., Jouanno, J.,  
1206 Körner, M., Roch, M., and Rouault, M.: Physical processes and biological productivity in the  
1207 upwelling regions of the tropical Atlantic, *Ocean Sci.*, 19, 581–601,  
1208 <https://doi.org/10.5194/os-19-581-2023>, 2023.
- 1209 Cabos, W., Sein, D. V., Pinto, J. G., Koseki, S., Álvarez-García, F. J., and Durán-Quesada, A. M.: The  
1210 coastal upwelling system of the southeast Atlantic as simulated by a high-resolution coupled model,  
1211 *Clim. Dynam.*, 49, 1809–1828, <https://doi.org/10.1007/s00382-016-3319-9>, 2017.
- 1212 Caniaux, G., Giordani, H., Redelsperger, J. L., Guichard, F., Key, E., and Wade, M.: Coupling between  
1213 the Atlantic cold tongue and the West African monsoon in boreal spring and summer, *J. Geophys. Res.*  
1214 *Oceans*, 116, C04003, <https://doi.org/10.1029/2010jc006570>, 2011.
- 1215 Carr, M.-E.: Estimation of potential productivity in Eastern Boundary Currents using remote sensing,  
1216 *Deep-Sea Res. Pt. II*, 49, 59–80, [https://doi.org/10.1016/S0967-0645\(01\)00094-7](https://doi.org/10.1016/S0967-0645(01)00094-7), 2002.
- 1217 Chavez, F. P. and Messié, M.: A comparison of eastern boundary upwelling ecosystems, *Prog.*  
1218 *Oceanogr.*, 83, 80–96, <https://doi.org/10.1016/j.pocean.2009.07.032>, 2009.
- 1219 Chin, T. M., Vazquez-Cuervo, J., and Armstrong, E.: A multi-scale high-resolution analysis of global  
1220 sea surface temperature, *Remote Sens. Environ.*, 200, 154–169,  
1221 <https://doi.org/10.1016/j.rse.2017.07.029>, 2017.
- 1222 de Boyer Montégut, C., Madec, G., Fischer, A. S., Lazar, A., and Iudicone, D.: Mixed layer depth over  
1223 the global ocean: An examination of profile data and a profile-based climatology, *J. Geophys. Res.*  
1224 *Oceans*, 109, C12003, <https://doi.org/10.1029/2004JC002378>, 2004.
- 1225 Bonhoure, D., Rowe, E., Mariano, A. J., and Ryan, E. H.: The South Equatorial Sys Current, *Ocean*  
1226 *Surface Currents*, available at: <https://oceancurrents.rsmas.miami.edu/atlantic/south-equatorial.html>  
1227 (last access: 18 February 2026), 2004.
- 1228 Dossa, A., Da-Allada, C., Herbert, G., and Bourlès, B.: Seasonal cycle of the salinity barrier layer  
1229 revealed in the northeastern Gulf of Guinea, *Afr. J. Mar. Sci.*, 41, 163–175,  
1230 <https://doi.org/10.2989/1814232X.2019.1616612>, 2019.

1231 Ducet, N., Le Traon, P.-Y., and Reverdun, G.: Global high-resolution mapping of ocean circulation  
1232 from TOPEX/Poseidon and ERS-1 and -2, *J. Geophys. Res. Oceans*, 105, 19477–19498,  
1233 <https://doi.org/10.1029/2000jc900063>, 2000.

1234 Dunn, J. R. and Ridgway, K. R.: Mapping ocean properties in regions of complex topography,  
1235 *Deep-Sea Res. Pt. I*, 49, 591–604, [https://doi.org/10.1016/S0967-0637\(01\)00069-3](https://doi.org/10.1016/S0967-0637(01)00069-3), 2002.

1236 Estival, R., Quiniou, V., and Messenger, C.: Real-time network of weather and ocean stations:  
1237 public-private partnership on in-situ measurements in the Gulf of Guinea, *Sea Technol.*, 54, 34–38,  
1238 2013.

1239 FAO: Fishery and Aquaculture Country Profiles, Angola, Country Profile Fact Sheets, Fisheries and  
1240 Aquaculture Division [online], available at: <https://www.fao.org/fishery/en/facp/ago?lang=en> (last  
1241 access: 11 April 2023), 2022.

1242 Fréon, P., Barange, M., and Arístegui, J.: Eastern boundary upwelling ecosystems: integrative and  
1243 comparative approaches, *Prog. Oceanogr.*, 83, 1–14, <https://doi.org/10.1016/j.pocean.2009.07.014>,  
1244 2009.

1245 Gutknecht, E., Dadou, I., Marchesiello, P., Cambon, G., Le Vu, B., Sudre, J., Garçon, V., Machu, E.,  
1246 Rixen, T., Kock, A., Flohr, A., Paulmier, A., and Lavik, G.: Nitrogen transfers off Walvis Bay: a 3-D  
1247 coupled physical/biogeochemical modeling approach in the Namibian upwelling system,  
1248 *Biogeosciences*, 10, 4117–4135, <https://doi.org/10.5194/bg-10-4117-2013>, 2013.

1249 Hardman-Mountford, N. J. and McGlade, J. S.: Retrieval of phytoplankton biomass from ocean colour  
1250 in the Benguela ecosystem, *Remote Sens. Environ.*, 79, 11–23,  
1251 [https://doi.org/10.1016/S0034-4257\(01\)00236-0](https://doi.org/10.1016/S0034-4257(01)00236-0), 2002.

1252 Hopkins, J., Lucas, M., Dufau, C., Sutton, M., Stum, J., Lauret, O., and Channelliere, C.: Detection  
1253 and variability of the Congo River plume from satellite derived sea surface temperature, salinity, ocean  
1254 colour and sea level, *Remote Sens. Environ.*, 139, 365–385, <https://doi.org/10.1016/j.rse.2013.08.015>,  
1255 2013.

1256 Hutchings, L., van der Lingen, C. D., Shannon, L. J., Crawford, R. J. M., Verheye, H. M. S.,  
1257 Bartholomae, C. H., van der Plas, A. K., Louw, D., Kreiner, A., Ostrowski, M., Fidel, Q., Barlow, R.  
1258 G., Lamont, T., Coetzee, J., Shillington, F., Veitch, J., Currie, J. C., and Monteiro, P. M. S.: The  
1259 Benguela Current: An ecosystem of four components, *Prog. Oceanogr.*, 83, 15–32,  
1260 <https://doi.org/10.1016/j.pocean.2009.07.046>, 2009.

1261 Johns, W. E., Brandt, P., Lumpkin, R., Fischer, J., Hormann, V., Pirani, A., Schmid, C., and Bourlès,  
1262 B.: Variation of upper ocean seasonal and interannual velocity structure in the eastern equatorial  
1263 Atlantic, *J. Phys. Oceanogr.*, 44, 1201–1212, <https://doi.org/10.1175/JPO-D-13-0132.1>, 2014.

1264 Johnson, E. S., Bonjean, F., Lagerloef, G. S., Gunn, J. T., and Mitchum, G. T.: Validation and error  
1265 analysis of OSCAR sea surface currents, *J. Atmos. Ocean. Tech.*, 24, 688–701,  
1266 <https://doi.org/10.1175/JTECH1971.1>, 2007.

1267 Jouanno, J.: Influence de la dynamique de l’Atlantique équatorial sur la variabilité de la langue froide,  
1268 PhD thesis, Université de Toulouse III, France, 2010.

- 1269 Kobayashi, S., Ota, Y., Harada, Y., Ebita, A., Moriya, M., Onoda, H., Onogi, K., Kamiguchi, H.,  
1270 Kobayashi, C., Endo, H., Miyaoka, K., and Takahashi, K.: The JRA-55 Reanalysis: General  
1271 specifications and basic characteristics, *J. Meteorol. Soc. Jpn.*, 93, 5–48,  
1272 <https://doi.org/10.2151/jmsj.2015-001>, 2015.
- 1273 Kopte, R.: The Angola Current in a Tropical Seasonal Upwelling System: Seasonal Variability in  
1274 Response to Remote Equatorial and Local Forcing, PhD thesis, Christian-Albrechts Universität Kiel,  
1275 Germany, 2017.
- 1276 Körner, M., Brandt, P., and Dengler, M.: Seasonal cycle of sea surface temperature in the tropical  
1277 Angolan Upwelling System, *Ocean Sci.*, 19, 121–139, <https://doi.org/10.5194/os-19-121-2023>, 2023.
- 1278 Körner, M., Brandt, P., Illig, S., Dengler, M., Subramaniam, A., Bachèlery, M. L., and Krahnemann, G.:  
1279 Coastal trapped waves and tidal mixing control primary production in the tropical Angolan upwelling  
1280 system, *Sci. Adv.*, 10, adj6686, <https://doi.org/10.1126/sciadv.adj6686>, 2024.
- 1281 Locarnini, M. M., Mishonov, A. V., Baranova, O. K., Boyer, T. P., Zweng, M. M., Garcia, H. E.,  
1282 Mishonov, A., and Smolyar, I.: World ocean atlas 2018, volume 1: Temperature, NOAA Atlas  
1283 NESDIS, 81, 2018.
- 1284 Koseki, S., Cabos, W., Sein, D. V., and Mohino, E.: The role of the Gulf of Guinea upwelling in the  
1285 atmospheric circulation of the tropical Atlantic in a high-resolution coupled model, *Clim. Dynam.*, 51,  
1286 1017–1035, <https://doi.org/10.1007/s00382-017-3896-2>, 2018.
- 1287 Koubanova, M., Koseki, S., and Keenlyside, N. S.: Seasonal variability of the Atlantic cold tongue and  
1288 its relationship with the Angola-Benguela upwelling system, *Clim. Dynam.*, 51, 2975–2993,  
1289 <https://doi.org/10.1007/s00382-018-4197-0>, 2018.
- 1290 Loukos, H. and Mémerly, L.: Simulation of the nitrate seasonal cycle in the equatorial Atlantic ocean  
1291 during 1983 and 1984, *J. Geophys. Res. Oceans*, 104, 15549–15573,  
1292 <https://doi.org/10.1029/1999JC900084>, 1999.
- 1293 Madec, G. and the NEMO System Team: NEMO Ocean Engine Reference Manual, Zenodo [code],  
1294 <https://doi.org/10.5281/zenodo.1464816>, 2024.
- 1295 Messié, M. and Chavez, F. P.: Seasonal regulation of primary production in eastern boundary  
1296 upwelling systems, *Prog. Oceanogr.*, 134, 1–18, <https://doi.org/10.1016/j.pocean.2014.10.011>, 2015.
- 1297 Monteiro, P., Dewitte, B., Scranton, M., Paulmier, A., and Van der Plas, A.: The role of open ocean  
1298 boundary forcing on seasonal to decadal-scale variability and long-term change of natural shelf  
1299 hypoxia, *Environ. Res. Lett.*, 6, 024002, <https://doi.org/10.1088/1748-9326/6/2/024002>, 2011.
- 1300 Ngakala, R. D., Alory, G., Da-Allada, C. Y., Dadou, I., Cardot, C., Morvan, G., and Baloïtcha, E.:  
1301 Seasonal mixed layer temperature in the Congolese upwelling system, *J. Geophys. Res. Oceans*, 130,  
1302 e2023JC020528, <https://doi.org/10.1029/2023JC020528>, 2025.
- 1303 Nieto, K. and Mélin, F.: Variability of chlorophyll-a concentration in the Gulf of Guinea and its  
1304 relation to physical oceanographic variables, *Prog. Oceanogr.*, 151, 97–115,  
1305 <https://doi.org/10.1016/j.pocean.2016.12.001>, 2017.

1306 Nubi, O., Bourles, B., and Edokpayi, C.: On the Nutrient distribution and phytoplankton biomass in  
1307 the Gulf of Guinea equatorial band as inferred from In-situ measurements, *J. Oceanogr. Mar. Sci.*, 7,  
1308 1–11, <https://doi.org/10.5897/JOMS2015.0125>, 2016.

1309 Ostrowski, M., da Silva, J. C. B., and Bazik-Sangolay, B.: The response of sound scatterers to El Niño-  
1310 and La Niña-like oceanographic regimes in the southeastern Atlantic, *ICES J. Mar. Sci.*, 66,  
1311 1063–1072, <https://doi.org/10.1093/icesjms/fsp102>, 2009.

1312 Radenac, M.-H., Jouanno, J., Tchamabi, C. C., Awo, M., Bourlès, B., Arnault, S., and Aumont, O.:  
1313 Physical drivers of the nitrate seasonal variability in the Atlantic cold tongue, *Biogeosciences*, 17,  
1314 529–545, <https://doi.org/10.5194/bg-17-529-2020>, 2020.

1315 Resplandy, L., Hogikyan, A., Müller, J. D., Najjar, R. G., Bange, H. W., Bianchi, D., and Regnier, P.: A  
1316 synthesis of global coastal ocean greenhouse gas fluxes, *Global Biogeochem. Cy.*, 38,  
1317 e2023GB007803, <https://doi.org/10.1029/2023GB007803>, 2024.

1318 Ridgway, K. R., Dunn, J. R., and Wilkin, J. L.: Ocean interpolation by four-dimensional least  
1319 squares—Application to the waters around Australia, *J. Atmos. Ocean. Tech.*, 19, 1357–1375,  
1320 [https://doi.org/10.1175/1520-0426\(2002\)019<1357:OIBFDL>2.0.CO;2](https://doi.org/10.1175/1520-0426(2002)019<1357:OIBFDL>2.0.CO;2), 2002.

1321 Rouault, M.: Bi-annual intrusion of tropical water in the northern Benguela upwelling, *Geophys. Res.*  
1322 *Lett.*, 39, L12606, <https://doi.org/10.1029/2012gl052099>, 2012.

1323 Scannell, H. A. and McPhaden, M. J.: Seasonal mixed layer temperature balance in the southeastern  
1324 tropical Atlantic, *J. Geophys. Res. Oceans*, 123, 5557–5570, <https://doi.org/10.1029/2018JC014099>,  
1325 2018.

1326 Schott, F. A., Fischer, J., and Stramma, L.: Transports and pathways of the upper-layer circulation in  
1327 the western tropical Atlantic, *J. Phys. Oceanogr.*, 28, 1904–1928,  
1328 [https://doi.org/10.1175/1520-0485\(1998\)028<1904:TAPOTU>2.0.CO;2](https://doi.org/10.1175/1520-0485(1998)028<1904:TAPOTU>2.0.CO;2), 1998.

1329 Siegfried, L., Schmidt, M., Mohrholz, V., Pogrzeba, H., Nardini, P., Böttinger, M., and Scheuermann,  
1330 G.: The tropical-subtropical coupling in the Southeast Atlantic from the perspective of the northern  
1331 Benguela upwelling system, *PLOS ONE*, 14, e0210083, <https://doi.org/10.1371/journal.pone.0210083>,  
1332 2019.

1333 Sikhakolli, R., Sharma, R., Basu, S., Gohil, B. S., Sarkar, A., and Prasad, K. V. S. R.: Evaluation of  
1334 OSCAR ocean surface current product in the tropical Indian Ocean using in situ data, *J. Earth Syst.*  
1335 *Sci.*, 122, 187–199, <https://doi.org/10.1007/s12040-012-0258-0>, 2013.

1336 Sowman, M. and Cardoso, P.: Small-scale fisheries and food security strategies in countries in the  
1337 Benguela Current Large Marine Ecosystem (BCLME) region: Angola, Namibia and South Africa,  
1338 *Mar. Policy*, 34, 1163–1170, <https://doi.org/10.1016/j.marpol.2010.03.016>, 2010.

1339 Tchupalanga, P., Dengler, M., Brandt, P., Kopte, R., Macueria, M., Coelho, P., Ostrowski, M., and  
1340 Keenlyside, N. S.: Eastern Boundary Circulation and Hydrography Off Angola: Building Angolan  
1341 Oceanographic Capacities, *B. Am. Meteorol. Soc.*, 99, 1589–1605,  
1342 <https://doi.org/10.1175/Bams-D-17-0197.1>, 2018.

1343 Thiam, A., Alory, G., Jouanno, J., Da-Allada, C. Y., and Morvan, G.: Coastal upwelling in the  
1344 Northern Gulf of Guinea: Seasonal cycle and mesoscale interactions, *Ocean Model.*, 188, 102300,  
1345 <https://doi.org/10.1016/j.ocemod.2024.102300>, 2024.

1346 Tilstone, G., Smyth, T., Poulton, A., and Hutson, R.: Measured and remotely sensed estimates of  
1347 primary production in the Atlantic Ocean from 1998 to 2005, *Deep-Sea Res. Pt. II*, 56, 918–930,  
1348 <https://doi.org/10.1016/j.dsr2.2008.10.034>, 2009.

1349 Topé, G. D. A., Alory, G., Djakouré, S., Da-Allada, C. Y., Jouanno, J., and Morvan, G.: How does the  
1350 Niger River warm coastal waters in the Northern Gulf of Guinea?, *Front. Mar. Sci.*, 10, 1187202,  
1351 <https://doi.org/10.3389/fmars.2023.1187202>, 2023.

1352 Tuchen, F. P., Brandt, P., Lübbecke, J. F., and Hummels, R.: Transports and pathways of the tropical  
1353 AMOC return flow from Argo data and shipboard velocity measurements, *J. Geophys. Res. Oceans*,  
1354 127, e2021JC018115, <https://doi.org/10.1029/2021JC018115>, 2022.

1355 Voldoire, A., Belamari, S., and Lévy, M.: On the role of ocean-atmosphere interaction in the onset of  
1356 the Atlantic cold tongue, *Clim. Dynam.*, 53, 5437–5455, <https://doi.org/10.1007/s00382-019-04717-0>,  
1357 2019.

1358 Xu, Z., Li, M., Patricola, C. M., and Chang, P.: Oceanic origin of southeast tropical Atlantic biases,  
1359 *Clim. Dynam.*, 43, 2915–2930, <https://doi.org/10.1007/s00382-013-1901-y>, 2014.

1360 Zeng, Z., Brandt, P., Lamb, K. G., Greatbatch, R. J., Dengler, M., Claus, M., and Chen, X.:  
1361 Three-dimensional numerical simulations of internal tides in the Angolan upwelling region, *J.*  
1362 *Geophys. Res. Oceans*, 126, e2020JC016460, <https://doi.org/10.1029/2020JC016460>, 2021.

1363 Zuidema, P., Redemann, J., Haywood, J., Wood, R., Piketh, S., Hipondoka, M., and Formenti, P.:  
1364 Smoke and clouds above the southeast Atlantic: Upcoming field campaigns probe absorbing aerosol's  
1365 impact on climate, *B. Am. Meteorol. Soc.*, 97, 1131–1135,  
1366 <https://doi.org/10.1175/BAMS-D-15-00032.1>, 2016.

1367 Zweng, M. M., Seidov, D., Boyer, T. P., Locarnini, M., Garcia, H. E., Mishonov, A. V., and Smolyar,  
1368 I.: World ocean atlas 2018, volume 2: Salinity, NOAA Atlas NESDIS, 82, 2019.

1369