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Bottom-up propagation of synoptic wind intensification and relaxation in the planktonic ecosystem of the South Senegalese Upwelling Sector

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Abstract

Synoptic intensification or relaxation of upwelling favorable winds are major sources of variability in Eastern Boundary Upwelling systems. This study aims to investigate their impact on the planktonic ecosystem of the South Senegalese Upwelling Sector (SSUS), located south of the Cape Verde peninsula over a wide and shallow continental shelf. Numerical experiments using a three dimensional coupled physical-biogeochemical model with four plankton functional types simulated the response of the coastal planktonic ecosystem to idealized synoptic (~10 days) wind intensification and relaxation of the same amplitude. We find that these perturbations induce spatio-temporal oscillations of plankton concentrations. Zooplankton response occurred with a time lag that manifests itself in space as an equatorward/downstream shift in distribution relative to phytoplankton. Overall, the transmission of the synoptic perturbation from the physics to zooplankton is characterised by a damping in relative anomalies. All these elements and the weakness of the asymmetries in the biogeochemical/planktonic ecosystem responses between intensification and relaxation events support the hypothesis that synoptic variability has limited impact on the climatological state of low-latitude upwelling systems such as the SSUS.

25 **Plain Language Summary**

26 In some coastal regions of the world such as off Senegal, winds preferentially blow alongshore and
27 induce subsurface, cold and nutrient rich waters to rise to the surface layer and favor the development of
28 plankton blooms. These so-called upwelling favorable winds are not steady. Their fluctuations produce
29 dynamical and biogeochemical variability over a broad range of scales. Here we studied the
30 biogeochemical effect of 10-day (i.e. weather or synoptic) wind fluctuations over the southern Senegal
31 continental shelf. We used a numerical model with a simplified planktonic ecosystem consisting of two
32 phytoplankton and two zooplankton size classes. The wind perturbations modulate ocean physics, the
33 enrichment of the sun-lit surface layer in nutrients and the planktonic ecosystem. The plankton's
34 response to wind fluctuations exhibited oscillations more complex and relatively less intense than those
35 of the wind. The modest effect of the studied short-term wind fluctuations on plankton found in this
36 study may be specific to low-latitude coastal oceans with wide continental shelves.

37 **1 Introduction**

38 Alongshore upwelling favorable winds provide eastern boundary upwelling systems with nutrient and
39 plankton rich surface waters, with great implications for the local and global fishing activities (Fréon et
40 al., 2009; Chavez & Messié, 2009). In addition to their seasonality and low frequency variability, these
41 winds fluctuate on synoptic (3-10 days) and intraseasonal (< 2 months) time scales. This fluctuation
42 affects the physics, carbon cycling, as well as the ecosystem dynamics of coastal upwellings (Largier et
43 al., 2006; Spitz et al., 2005; Desbiolles et al., 2014; Capet et al., 2017; Galán et al., 2020; Aguirre et al.,
44 2021). In our domain of interest offshore of West Africa the shorter synoptic time scale tends to
45 dominate over longer ones (Tall et al., 2021). We will thus restrict our attention to this range of scales.
46 Synoptic variability consists of a succession of intensifications and relaxations of upwelling favorable
47 winds. Associated modulations of the Ekman transport and wind stress curl (hence also of Ekman
48 pumping and lateral Sverdrup transport), and of mixing rates and stratification (Largier et al., 2006;
49 Jacox & Edwards, 2011) are the most common ways physics affect marine primary production and food
50 webs. Previous studies have uncovered situations in which synoptic wind variability produced flow
51 disturbances that have plausibly large implications on plankton dynamics and the reproductive strategies
52 of many marine animals (Botsford et al., 2003, 2006).
53 The effect of synoptic variability on primary production, and more generally on the functioning of

54 upwelling ecosystems is not well understood. (Largier et al., 2006) and (Wilkerson et al., 2006)
55 described the importance of sequences involving an upwelling wind intensification (inducing a pulse of
56 nutrients in the euphotic layer) followed by a wind relaxation (leading to restratification and a plankton
57 bloom). In the idealized 2D vertical setting of Botsford (Botsford et al., 2006) synoptic variability could
58 be beneficial or detrimental to bulk primary/secondary production of a continental shelf. In an upwelling
59 sector where average winds are high and/or the shelf is narrow wind relaxation periods allowed for an
60 intermittently better utilization of upwelled nutrients. Conversely, in a system where average winds are
61 low and/or the shelf is relatively wide, strong episodic upwelling events generally accelerated offshore
62 export and/or subduction of upwelled nutrients (Evans et al., 2015) which may not have been converted
63 into plankton biomass. This conceptual landscape is broadly consistent with the evidence of optimal
64 wind windows for primary production and plankton stock (Yokomizo et al., 2010; Jacox et al., 2016).
65 Beside shelf width and wind regime, the oceanic response to synoptic variability depends on the
66 specificities of each upwelling sector. These specificities include coastline geomorphological
67 irregularities which exert important constraints on the flow (Largier, 2020; Spitz et al., 2005),
68 (sub)mesoscale turbulence regime which can have a leading order effect on premature subduction of
69 upwelled nutrients (Gruber et al., 2011; Renault et al., 2016; Hauschildt et al., 2021; Nagai et al., 2015),
70 nearshore productivity and biomass/carbon export (Stukel et al., 2017; Chabert et al., 2021).
71 The continental shelf on which we focus, the southern Senegalese upwelling sector (SSUS), extends over
72 approximately 5 degrees of latitude south of Dakar. Among its prime characteristics are a sharp
73 coastline discontinuity toward its northern edge, a wide continental shelf further south (see Fig. 1), and
74 low-to-moderate upwelling winds.

75 All this plays in favor of long retention time scales in comparison to other areas subjected to upwelling
76 dynamics (Ndoye et al., 2017). Based on a qualitative application of Botsford's reasoning (Botsford et
77 al., 2006), synoptic variability could strengthen offshore export during wind intensifications, leading to
78 an overall deterioration of the retentive properties of the system. In more quantitative terms though, it is
79 unclear if the acceleration of the upwelling flow during typical upwelling wind events can be sufficient to
80 produce retention changes with a significant impact on coastal primary and secondary production.

81 In this study, our objective is to gain insight into the effect of synoptic variability of atmospheric forcings
82 on the SSUS plankton dynamics. Specifically, we describe the cascade of the synoptic perturbation from
83 physics to zooplankton (*e.g.*, the existence of damping or amplification between trophic levels), and
84 characterise the asymmetries between the response to upwelling relaxation and intensification events (as

85 previously done for ocean physics, see (Chabert et al., 2023)). Quantifying asymmetric behaviours
86 provides useful indications on the degree to which net rectification effects of synoptic variability (i.e.,
87 compensations between wind intensification and relaxation responses accounted for) impact the mean
88 state and functioning of the real ocean (more details are given in section 2.5).
89 To do so we carried out 3D physics-biogeochemistry model experiments. The plankton ecosystem
90 consisted of two phytoplankton and two zooplankton types. One deliberate model simplification
91 concerned the synoptic fluctuations of the atmospheric forcing which were constructed so as to ensure
92 perfect symmetry between wind intensification and relaxations events, thereby facilitating the
93 identification of sources of asymmetry internal to the ocean. Having chosen to explore the effect of
94 synoptic fluctuations of rather extreme magnitude, we found substantial plankton responses to them with
95 biomass changes of $\pm 20-50\%$. However there was an overall attenuation of the synoptic disturbances as
96 they propagated from physics to zooplankton and also a relatively low degree of asymmetry between the
97 responses, hence our general conclusion on the limited role played by synoptic variability in the SSUS.
98 Section 2 presents the methods and section 3 the model mean state (evaluation of the model using
99 observations is shown in the supplementary material). The model response to symmetric atmospheric
100 forcing anomalies is examined in sections 4 and 5. We describe in sequence: the domain-wide temporal
101 evolution of the response during and after the synoptic fluctuations (section 4a); the disturbances of the
102 spatial patterns produced within the SSUS (section 4b); and the bottom-up propagation of the synoptic
103 anomalies (section 5). A discussion and some concluding remarks are given in section 6.

104 **2 Modelling framework and methods**

105 The framework described below was designed with the following specifications in mind: to preserve the
106 degree of realism achieved by the configuration/setup used in (Ndoye et al., 2017); to add synoptic
107 perturbations of the wind and net heat flux forcings representative of major upwelling intensification and
108 relaxation events; to transition smoothly from climatological to synoptic forcing; to be able to identify
109 the forced ocean response despite the turbulent nature of its dynamics. The former specification led us to
110 use distinct atmospheric products for the climatological and synoptic anomaly components of the
111 forcing. The latter motivated the computation of ensemble runs.

112 **2.1 Physical and biogeochemical models**

113 We developed a modelling framework based on an ensemble of perturbed coupled
114 physical-biogeochemical simulations forced by an idealized synoptic forcing. Analysing the ensemble
115 mean and spread reduced the effect of intrinsic variability permitting identification of the robust
116 components of the synoptic responses. To model the ocean dynamics, we used the Coastal and Regional
117 Ocean COmmunity model (CROCO, from <https://www.croco-ocean.org/>; Hilt et al. (2020)),
118 derived from Regional Ocean Modeling System (ROMS; Shchepetkin and McWilliams (2005, 2009)).
119 CROCO solves the primitive equations for a free-surface ocean in an earth-centered rotating
120 environment. Its high-order numerical schemes and terrain-following vertical coordinates allow for a
121 realistic representation of the fine scale fronts and flows prevalent in coastal environments. The
122 K-Profile Parameterization (KPP; Large et al. (1994)) was used as vertical mixing scheme.
123 CROCO was coupled to the marine biogeochemistry model Pelagic Interactions Scheme for Carbon and
124 Ecosystem Studies (PISCES, from <https://www.pisces-community.org/>; Aumont et al. (2015)).
125 The latter represents the main nutrients (nitrate, phosphate, silicate and iron) and has four size-structured
126 living compartments: nanophytoplankton (NANO), microzooplankton (MICRO), diatoms (DIA) and
127 mesozooplankton (MESO). The size range of the diatom group is typically 5-80 μm . The vertical
128 distribution of solar heating in the water column is influenced by the three-dimensional phytoplankton
129 chlorophyll concentration field inducing horizontally inhomogeneous biomass-dependent thermal
130 heating (Echevin et al., 2021).
131 The model configuration was inherited from (Ndoye et al., 2017) and (Chabert et al., 2023): a parent
132 grid (can11) covering the Canary current system [32°W-6°W,7°N-36°N] with a spatial resolution of ~ 10
133 km and a child grid (sen2) centered on the Senegalese sector [20°W-16°W,12°N-18°N] at ~ 2.5 km were
134 coupled using AGRIF two-way nesting (Debreu & Blayo, 2008). Both model domains use the same
135 vertical grid parameters and 50 levels.

136 **2.2 Generation of an ensemble of initial states**

137 A climatological simulation was performed. It was forced at the air-sea interface by monthly
138 climatological surface heat and freshwater fluxes from the International Comprehensive Ocean
139 Atmosphere Data Set (COADS; years 1854-1992; spatial resolution $\Delta x = 0.5^\circ$; Worley et al. (2005)),
140 monthly SST from the Moderate Resolution Imaging Spectroradiometer (MODIS; years 2002-2018;
141 $\Delta x = 5$ km; NASA (2014)) for SST restoring (Barnier et al., 1995), and monthly wind stress from the

142 Scatterometer Climatology of Ocean Winds (SCOW; 1999-2009; $\Delta x = 0.25^\circ$; Risien and Chelton
143 (2008)). A monthly climatology (2000-2008 period) of the Simple Ocean Data Assimilation (SODA;
144 Carton and Giese (2008)) was imposed at the open boundaries. Initial conditions for the physical
145 variables were provided from a previous simulation having reached equilibrium (Ndoye et al., 2017).
146 For biogeochemical initial and boundary conditions, the World Ocean Atlas (WOA) climatology for
147 nitrate, phosphate, silicate and oxygen (Garcia et al., 2018), the Global Data Analysis Project
148 (GLODAP) climatology for dissolved inorganic and organic carbon (Key et al., 2004) and the
149 climatological dust deposition of Tegen and Fung (Tegen & Fung, 1994) were used.
150 This climatological simulation was run for 7 years and reached statistical equilibrium after 2 years (see
151 Supplementary Fig. 1). For each of the last 5 years of climatological simulation, restart states
152 corresponding to March 1st were stored to initialize the synoptic ensemble runs. The physical and
153 biogeochemical variables in these initial states differ due to the intrinsic chaotic variability of the
154 non-linear coupled model. Ensemble averaging over the 5-member ensemble run was systematically
155 performed for all fields shown or discussed. A brief evaluation of key biogeochemical variables (surface
156 chlorophyll-a and nitrate, averaged over the upwelling season (January-March) for the last 5 years of
157 simulation) is presented in the supplementary material (Figs. 2-4) .

158 **2.3 Idealized synoptic forcing**

159 The idealized synoptic forcing is defined as follows. The forcing anomaly consists of a spatial pattern
160 $\phi'_{SF}(x, y)$ multiplied by a temporal amplitude modulation $f(t)$. The anomaly was added to the
161 climatological forcing ϕ_{clim} as defined in Eq. 1:

$$\phi_{SF^\pm}(x, y, t) = \phi_{clim}(x, y, t) \pm f(t) \times \phi'_{SF}(x, y) \quad (1)$$

162 with ϕ an atmospheric forcing variable (wind stress or air-sea net heat flux). $\phi'_{SF}(x, y)$ and $f(t)$ were
163 built using ERA5 reanalyses (Hersbach et al., 2018). By construction the synoptic intensification and
164 relaxation anomalies were symmetric. Having perfectly symmetric SF^+ and SF^- forcings ensures that
165 any asymmetry in the ocean state and functioning is produced by nonlinearities internal to the system. In
166 nature or more realistic models, sources of asymmetry other than that considered are present, for
167 instance when atmospheric forcings are represented with a bulk formula, as symmetric wind fluctuations
168 would produce asymmetric wind stress and heat flux perturbations.

169 The amplitude of these anomalies was modulated in time ($f = f(t)$) over a 10-day window with a ramp

170 up, a plateau and a ramp-down back to 0 (see grey dashed line in Fig. 3a). The amplitude of the
171 perturbation was determined using the distribution of 10-day averaged intraseasonal wind stress
172 anomalies in ERA5 (see Table 1 for the wind and Fig. 2 in (Chabert et al., 2023)). The net air-sea heat
173 flux perturbation was of the order of $\pm 30 \text{ W.m}^{-2}$, *i.e.*, comparable to the net flux itself at that season (\sim
174 $30\text{-}40 \text{ W.m}^{-2}$), but with limited spatial contrasts and therefore a modest dynamical impact (Chabert et
175 al., 2023). Our wind anomalies ($\pm 0.032 \text{ N.m}^{-2}$) roughly belonged to the 95th percentile of the
176 distribution (see Table 1). Although it may seem extreme, this choice is appropriate to produce a
177 significant response of the ecosystem to the wind synoptic fluctuations.

178 The symmetric atmospheric perturbations, an upwelling favorable wind intensification (positive
179 Synoptic Forcing perturbation: SF^+) and a relaxation (negative Synoptic Forcing perturbation: SF^-),
180 were added to the climatological forcing and used to force the ensemble simulations, starting on 1 March
181 (day 0 in our analysis). The reference simulations without perturbation (corresponding to the
182 climatological simulation) are denoted SF^0 . Additional information about how we ensured a smooth
183 transition from climatological to synoptic forcings and how we dealt with net heat flux anomalies can be
184 found in (Chabert et al., 2023).

185 **2.4 Tracer tendency terms**

186 To help interpret the synoptic evolution of the biogeochemical tracers of interest for our study (*i.e.* NO_3 ,
187 NANO, DIA, MICRO, MESO), we used budget analyses in which tendency for any variable X was
188 decomposed as:

$$\partial_t X = F_X^{Phy} + F_X^{Bio} \quad (2)$$

189 where F_X^{Phy} and F_X^{Bio} are respectively the lumped physical (advection and mixing) and biogeochemical
190 tendency terms stored online during the model computation and output at daily frequency. Time series
191 of these terms averaged over the shelf are analyzed in the following sections.

192 **2.5 Synoptic response indicators**

193 There have been frequent suggestions that (zero-mean) synoptic variability of atmospheric forcings
194 could have an important effect on the mean state of upwelling systems (Send et al., 1987; Wilkerson et
195 al., 2006; Iles et al., 2012). The simplest way this can happen is if the ocean responses to upwelling wind
196 intensification and relaxation are not fully symmetric. This is precisely what our model framework

197 allowed us to investigate. To quantify the net residual/rectification effects due to synoptic variability of
 198 atmospheric forcings, we determined the degree of asymmetry of the SF^\pm simulations relative to the
 199 climatological reference SF^0 . This was done by computing a residual index defined as
 200 $\mathcal{R}_{SF}(X) = \frac{\frac{1}{2}(X_{SF^+} + X_{SF^-})}{X_{SF^0}} - 1$ for any model variable X . To account for the history of the synoptic
 201 responses, we present cumulative averages of \mathcal{R}_{SF} (expressed in %) from the onset of the synoptic
 202 perturbation: $\mathcal{S}_{SF}(X, T) = \frac{1}{T} \int_0^T \mathcal{R}_{SF}(X) dt$. By construction, $\mathcal{S}_{SF}(X, T) \approx 0$ at $T=30$ days (i.e. the end of
 203 SF experiments when synoptic responses have faded away) would mean that a synoptic forcing
 204 combining an equal proportion of SF^\pm events with no interplay between the events has a negligible net
 205 effect on X , relative to the magnitude of its climatological state.

206 We are also interested in comparing the magnitude of the ocean response to SF^\pm for the different
 207 biogeochemical variables. To this end, we introduced $\mathcal{W}^{\pm 0}(X) = \left(\frac{X_{SF^\pm} - X_{SF^0}}{X_{SF^0}} \right)_{[t_1(X):t_2(X)]}$, which
 208 indicates the relative anomaly of X averaged over the 3-day interval $[t_1(X) : t_2(X)]$ chosen when
 209 variable X was most perturbed during the SF simulations (intervals are indicated for each variable in the
 210 upper part of each panel in Fig. 2). For each member i , the relative anomaly $\mathcal{W}_i^{\pm 0}$ is computed. The
 211 ensemble mean of this indicator is also plotted (see Fig. 5).

212 **3 Physical and planktonic ecosystem mean states**

213 The dynamics of the SSUS was strongly constrained by the geomorphology of the area. In short, robust
 214 spatial hydrological features existed during the upwelling season: i) a cold upwelling wake that
 215 originated south of the Cape Verde peninsula ($\sim 14.7^\circ N$) and approximately followed the 20-30 m
 216 isobath over a meridional distance of 100 km or more (Fig. 1a,d; see also Ndoye et al. (2017); Chabert et
 217 al. (2023)); ii) a relatively warm inshore strip over the inner shelf where bottom friction checked Ekman
 218 dynamics (through merging of the surface and bottom boundary layers (Estrade et al., 2008)) and
 219 enhanced residence times; iii) a warm anticyclonic meander/eddy that frequently impinged onto the
 220 continental shelf south of Dakar and whose southern edge coincides with a recurrent upwelling filament
 221 responsible for offshore export. These patterns resulted to a large extent from the continental shelf
 222 widening near $14.5^\circ N$ where preferential onshore water transport took place (Ndoye et al., 2017;
 223 Pringle, 2002). Our model was able to qualitatively reproduce these patterns and their disturbances by
 224 synoptic wind fluctuations with a degree of realism that we deemed sufficient to deserve analysis of its
 225 coupled biogeochemical solutions.

226 The zonation of the SSUS mean biogeochemical fields was also evident in Fig. 1. Elevated nitrate
227 concentrations and low SST were essentially colocated near the 20 m isobath while the inner shelf was
228 depleted of nitrate. The largest plankton concentrations were also located near the 20 m isobath, albeit a
229 bit on its onshore side north of 13.5-14°N (see Figs. 1b-f, note that all planktonic variables were
230 converted from carbon to nitrogen units using the model Redfield ratio 122/16 to facilitate comparison
231 with nitrate). We interpreted this as a consequence of enhanced retention and regenerated primary
232 production over the inner shelf.

233 The distribution of biogeochemical tracers revealed interesting alongshore structures consistent with
234 upwelling of nutrient-rich waters being concentrated just south of the peninsula (Figs. 1d and 2d green
235 line), and robust southward advection (Figs. 1a and 2a green line) while bottom-up trophic transfer
236 occurred.

237 Along this advection route, the temporal lags associated with the propagation of synoptic nutrient
238 anomalies through the trophic chain produced alongshore shifts in the plankton patterns. The
239 fast-growing NANO peaked earlier in time than the other plankton species, thus upstream (north) along
240 the mean advection pathway. Because of grazing, a relatively low NANO (resp. MICRO) abundance
241 was also found in the latitude range 13.5-14.2°N (resp. 13-13.5°N) where MICRO and MESO (resp.
242 MESO) concentrations became elevated. Overall, Figs. 1 and 2 revealed spatial oscillations in plankton
243 abundance which seemed consistent with prey-predator dynamics (Edwards & Brindley, 1996).
244 Additionally, we noted the unsurprising dominance of DIA over NANO in the nutrient-rich coastal area
245 (Fig. 1b,e; Hutchings et al. (1995); Irigoien et al. (2005)) and the modest role seemingly played by the
246 cold filament (situated near 13.5-14°N) on plankton export. We saw the latter as a direct consequence of
247 having high plankton concentrations slightly inshore of the cold plume, i.e, more sheltered from the
248 (sub)mesoscale export currents than the low temperature/high nutrient upwelled waters.

249 **4 Responses to synoptic forcing perturbations**

250 **4.1 Domain-wide temporal response**

251 Shelf-wide temporal responses of nitrate and plankton were examined by spatially averaging
252 biogeochemical tracer concentrations over the entire shelf (between latitudes 13-14.75°N from the coast
253 to the 100 m isobath; see grey box in Fig. 1a). The temporal modifications of concentration were
254 robustly out of the range of their intrinsic variability (Figs. 2 and 3). Nitrate and plankton concentrations

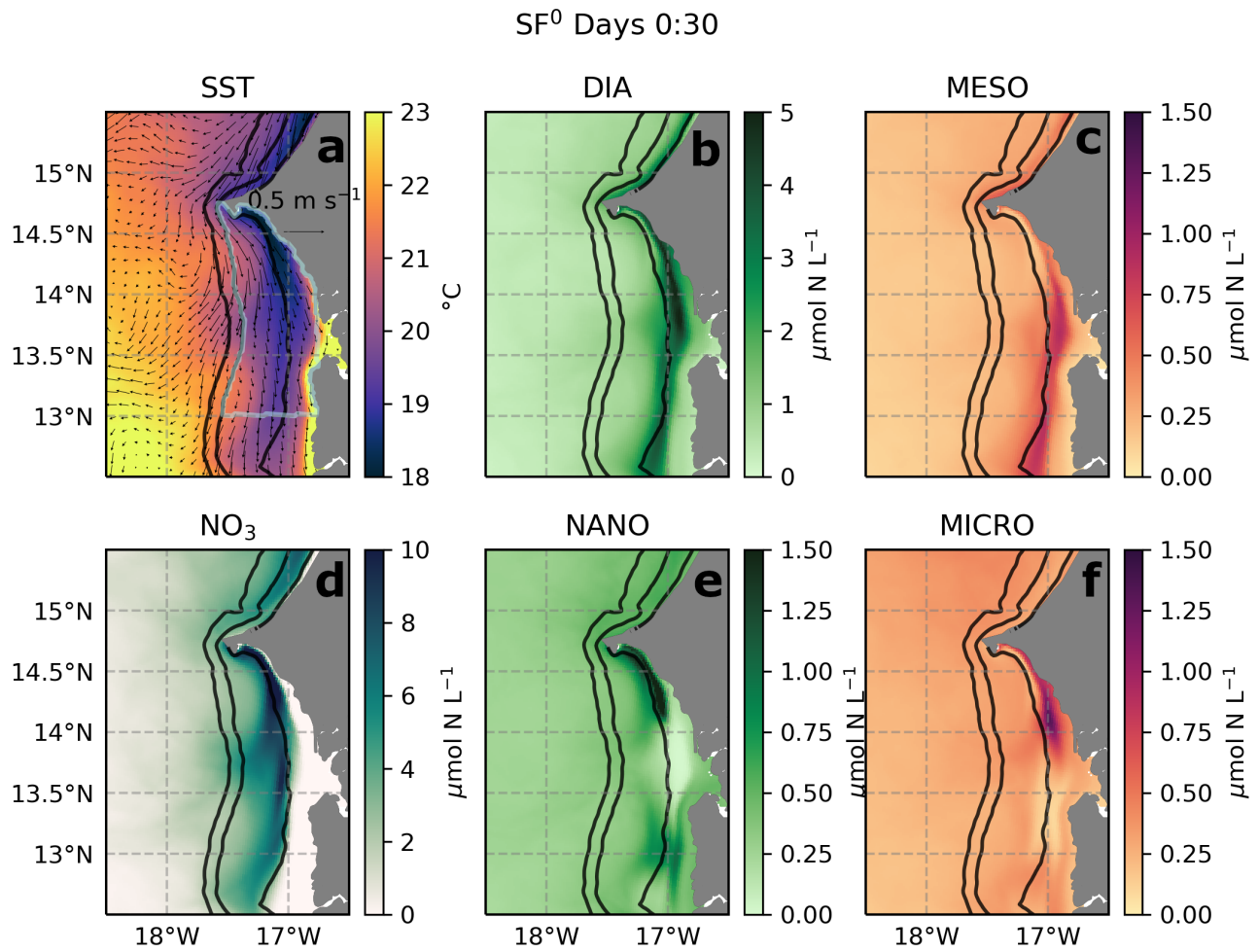


Figure 1: Surface patterns of SST (a), NO_3 (d), diatoms (b), nanophytoplankton (e), mesozooplankton (c) and microzooplankton (f) concentrations averaged over the ensemble for SF⁰ between days 0 and 30. The box on which variables are averaged spatially is indicated with the light grey contour on panel a. The black lines indicate the 20, 100 and 500 m isobaths. Note that colorbar ranges are different for diatoms and nanophytoplankton. The Cape Verde (CV) is the land promontory extending westward at 14.7°N.

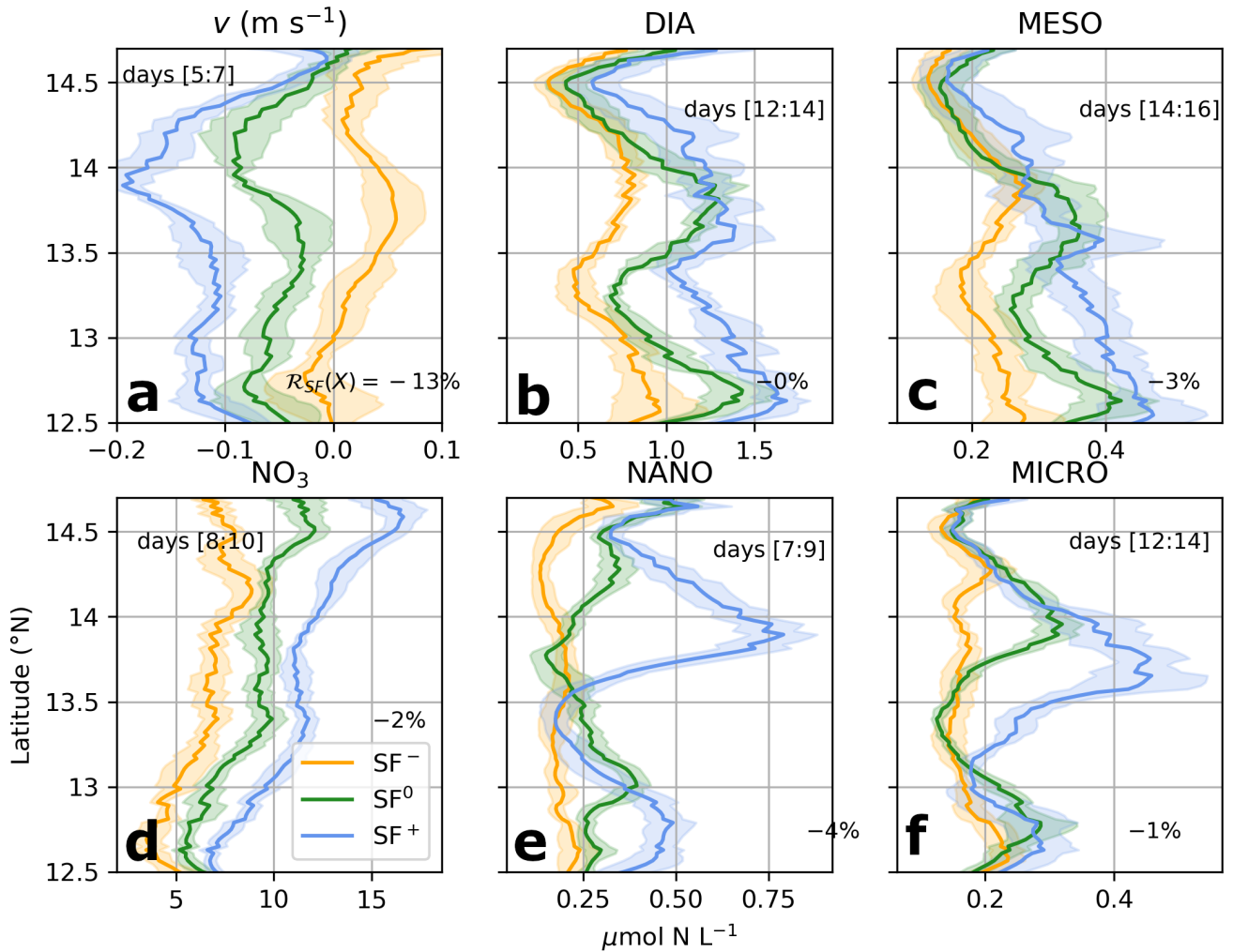


Figure 2: Meridional velocities (a), NO_3 (d), diatoms (b), nanophytoplankton (e), mesozooplankton (c) and microzooplankton (f) concentrations averaged over the entire shelf by latitude band (within the 100-0 m isobaths (see Fig.1) and from the bottom of the water column to the surface) and over the ensemble. SF^- , SF^0 and SF^+ are indicated in orange, green and blue lines; and the respective ensemble standard deviations are indicated by the shaded areas. \mathcal{R}_{SF} (see section 2.5) is indicated for each quantity on the bottom right side of each panel. The temporal intervals $[t_1(X) : t_2(X)]$ used for averages are indicated in the upper part of each panels.

255 tended to increase during SF^+ and decrease during SF^- , but magnitudes, time scales/timing relative to
256 that of the forcing anomaly, and details of synoptic responses were specific to each variable (see Fig. 3).
257 In particular, plankton responses to SF^\pm included several large oscillations unseen in the wind forcing
258 anomalies and nutrient response.

259 We start with the timing sequence. For SF^+ , the maximum value of nitrate was reached at day 9,
260 nanophytoplankton at day 11, diatoms at day 13, microzooplankton at day 15 and mesozooplankton at
261 day 17 (each planktonic extremum was reached broadly ~ 2 days earlier for SF^-). All plankton
262 concentrations (except nanophytoplankton) presented first a weak decrease (resp. increase) in the first
263 days of SF^+ (resp. SF^-), followed by a strong increase (resp. decrease) toward and after the end of the
264 wind perturbation. The small early peaks appeared on time scales shorter than those of planktonic
265 growth and were thus driven by ocean physics as an examination of budget terms revealed (Fig. 4; net
266 tendencies in plankton concentration evolved mainly due to changes in the physics during the first days
267 of the synoptic perturbation). The underlying process could only be the synoptic modulation of lateral
268 tracer fluxes in and out of our continental shelf control volume because budgets in Fig. 4 were vertically
269 averaged and therefore unaffected by vertical processes. NANO behaved differently because its shorter
270 growth time scale left little time for advection processes to dominate. Conversely, longer growth time
271 scales associated with large plankton (DIA and MESO) were consistent with their slower responses to
272 the main nutrient perturbation, relative to those of small plankton groups NANO and MICRO (Fig. 3;
273 and see section 5).

274 Another interesting aspect of the plankton response concerned the transition from SF^- back to
275 climatological conditions for NANO and MICRO, which exhibited an additional oscillation in the form
276 of an upward production rebound. This oscillation was absent in SF^+ whose intensification peak was, on
277 the other hand, more pronounced than the main relaxation trough in SF^- , hence a substantial SF^+/SF^-
278 asymmetry overall (see Fig. 3k,l).

279 Inspection of the budget terms indicated that a transient F_{NANO}^{Bio} excess around days 12-18 drove this SF^-
280 extra oscillation (see Fig. 4d). Conversely, ocean physics could not be an important driver since F_{NANO}^{Phy}
281 remained a one-signed (positive) anomalous source of NANO over the entire simulation. Given this and
282 the appropriate phase relationship between NANO and its predators, we thus concluded that our synoptic
283 forcing acted at temporal scales such that a (damped) prey-predator oscillation (Edwards & Brindley,
284 1996; Wang & Mu, 2014; Blasius et al., 2020) was produced between NANO and its fast predator
285 MICRO. Constraints on ocean physics must however exist to allow a 0-D prey-predator interaction to

286 take place in a 3-D moving environment where advection and mixing can weaken the strength of trophic
287 coupling. In fact, note that F_{NANO}^{Phy} did change sign and appeared in phase opposition relative to F_{NANO}^{Bio}
288 during SF^+ simulations (see Fig. 4f). This is how we rationalize the fact that no post-intensification
289 NANO-MICRO (negative) oscillation was found in SF^+ simulations, in which the circulation was
290 significantly more energetic than in SF^- (Fig. 3a).

291 Stronger currents in SF^+ leading to weaker trophic coupling/top-down control could also explain the
292 more intense forced reaction of NANO to SF^+ than SF^- (with respective \mathcal{W}^+ and \mathcal{W}^- values of 46 and
293 35 %). On the other hand, PISCES has several nonlinear features that prevent phytoplankton
294 concentrations from becoming too low (grazing refuge, density dependant mortality) and could be
295 responsible for this asymmetry. Untangling these physical and biogeochemical reasons would require
296 sensitivity runs.

297 We finish this section with a more quantitative assessment of asymmetries relative to the climatological
298 reference state. In Fig. 3d-f,j-l we show the evolution of the cumulative asymmetry index \mathcal{S}_{SF} (see
299 section 2 on methods). We have previously established in Chabert et al. (2023) that meridional velocities
300 exhibited the strongest asymmetries of all model physical variables, with $\mathcal{S}_{SF}(v)$ of the order of 10%
301 (Fig. 3d). Biogeochemical asymmetries were systematically lower than the latter, in particular at final
302 time. The ensemble spread was also quite diminished. And note that, despite being visually quite
303 affected by perturbations of the flow field, nitrate presented strikingly low asymmetry at SSUS scale
304 ($< 2\%$). Despite using intense wind perturbations (see section 2), the nonlinearities susceptible to
305 produce SF^\pm asymmetries, *e.g.*, through tracer advection, entrainment/detrainment in and out of the
306 mixed layer, or biogeochemical reactions, were thus essentially muted from a SSUS-wide system
307 perspective.

308 **4.2 Alongshore structure of the response**

309 SF^\pm perturbations modified the spatial distribution of plankton concentrations and in particular their
310 alongshore modulation described in section 3 (Fig. 2). SF^\pm anomalies are shown for the 2-day period
311 during which they were the most pronounced. All ecosystem quantities were significantly perturbed
312 spatially at these times.

313 During SF^+ , the most perturbed quantities were the concentrations of small plankton classes. The
314 NANO concentration maximum shifted southwards from 14.25 to 13.8°N (~ 50 km) and tripled in
315 amplitude. The peak in MICRO shifted from 14 to 13.6°N and increased by $\sim 50\%$ compared to SF^0 . It

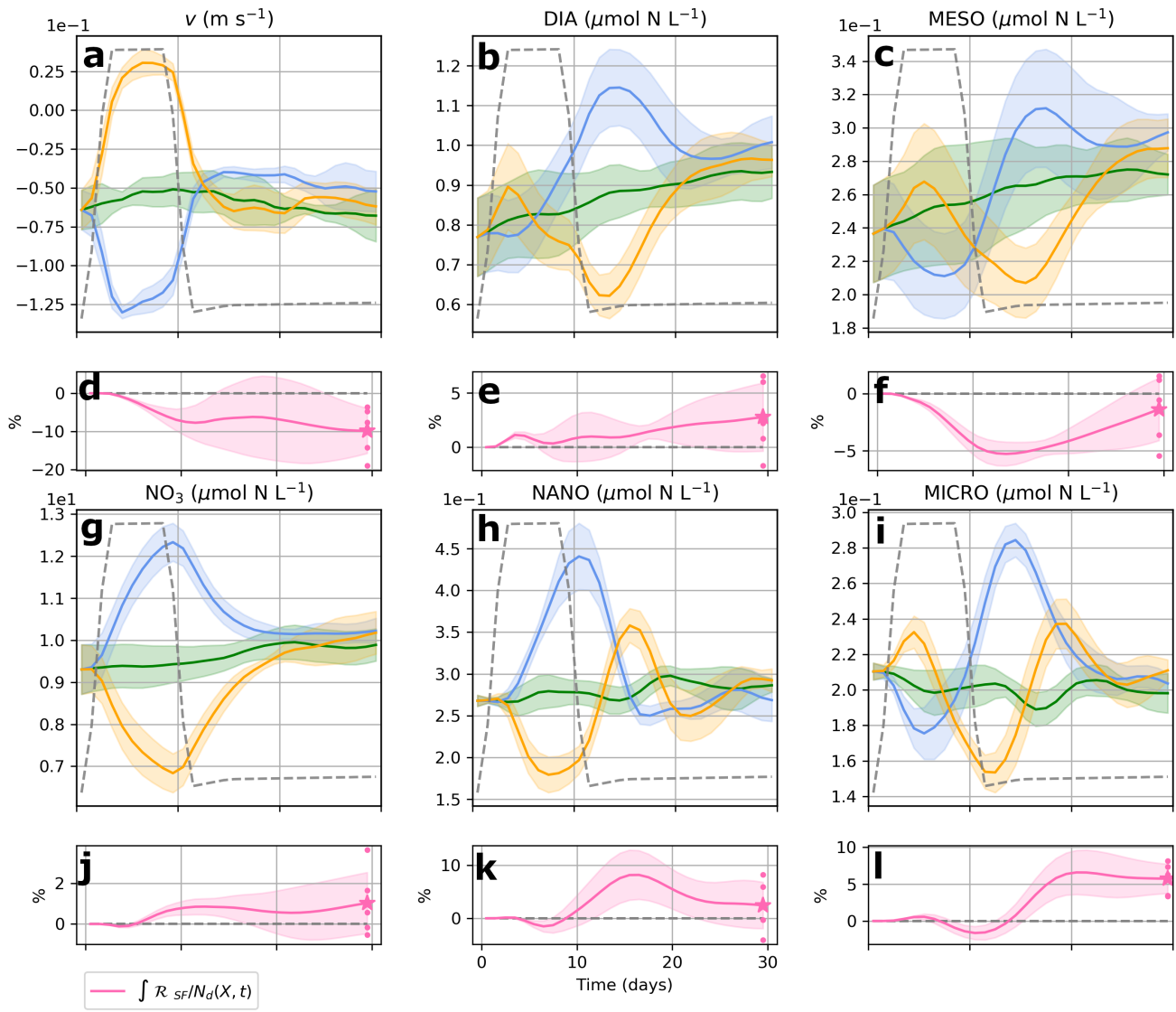


Figure 3: Meridional velocities (a), NO_3 (g), diatoms (b), nanophytoplankton (h), mesozooplankton (c) and microzooplankton (i) concentrations averaged over the entire shelf, water column, and over the ensemble. Green, orange and blue lines indicate SF^0 , SF^- and SF^+ . Shaded areas indicate the ensemble standard deviation. The box of integration is shown on Fig. 1a (grey contour between $13\text{-}14.75^\circ\text{N}$ and $0\text{-}100$ m isobaths). Time series of $\int \mathcal{R}_{\text{SF}}/N_d$ (with N_d the number of days) diagnose the perturbations asymmetries and are shown for each variable X in pink in panels (d-f,j-l); the value of each member of the ensemble at day 30 is indicated by a pink dot; each residual diagnostic panel is located below the panel showing the evolution of variable X . The grey dashed line indicates the amplitude modulation of the wind fluctuations. Note the different y-axis scales indicated on the top left of each panel.

316 even slightly exceeded the mesozooplankton concentration at this location. In contrast, changes in the
317 concentration of DIA and MESO occurred mostly south of 13.5°N. All this was consistent with the
318 notable increase in southward current (Fig. 2a) and its Lagrangian implications for the spatial
319 organization of trophic transfers. In the same spirit, note the small spatial shift between the SF⁺ peaks in
320 NANO (13.9°N) and MICRO (13.6°N), its main grazer.

321 During SF⁻, all spatial oscillations were damped such that plankton concentrations were more
322 homogeneous over the shelf compared to SF⁰. Currents were weaker and also more variable in SF⁻,
323 particularly in the south (Chabert et al., 2023). Modest peaks in DIA and MESO remained noticeable
324 but their location was shifted northward compared to SF⁰, again in agreement with the meridional
325 (northward) flow anomaly.

326 **5 Propagation of physical perturbations through the planktonic** 327 **ecosystem**

328 In this section, we investigate the trophic propagation of the disturbances to assess whether the bottom-up
329 perturbations are amplified or damped from one system level to the next. Fig. 5 displays \mathcal{W}^{\pm} , the relative
330 amplitude of the synoptic perturbations over the most perturbed period of the simulation (see section 2)
331 for the key variables concerned. The maximum amplitude of the absolute perturbations and the
332 underlying perturbations of transfer rates are also informative of trophic propagation (see Figs. 3 and 4).
333 We start with the transfer of the perturbation from wind to NO₃ enrichment. Based on a conceptual
334 Ekman/Bakun type model a classical *a priori* assumption to be used as a strawman is that \mathcal{W}^{\pm} for wind
335 stress and physical nitrate flux into the control volume ($F_{NO_3}^{Phy}$) are linearly related (Messié et al., 2009);
336 see for instance (Jacox et al., 2018; Jorgensen et al., 2024) for a more elaborate approach). Reasoning on
337 SF⁺, this would imply that increasing wind intensity by 60% leads to a relative increase of $F_{NO_3}^{Phy}$ by a
338 similar figure, and likewise in terms of decrease for SF⁻. In contrast, the system response was
339 characterized by the fact that: i) $\mathcal{W}^{\pm}(F_{NO_3}^{Phy})$ reached $\sim \pm 100\%$ at day 3 (compare panels a and c in
340 Fig. 4 to panel b), *i.e.*, wind perturbations were initially more effective in terms of NO₃ enrichment than
341 the climatological wind; ii) the extra NO₃ enrichment associated with the wind perturbation rapidly
342 diminished. Alongshore adjustment of the pressure field (sea level) by coastal trapped waves is an
343 important factor shaping the response of coastal systems to wind forcing at various time scales
344 (Philander & Yoon, 1982; Ndoye et al., 2017; Colas et al., 2008). The early response of $F_{NO_3}^{Phy}$ to SF⁺/SF⁻

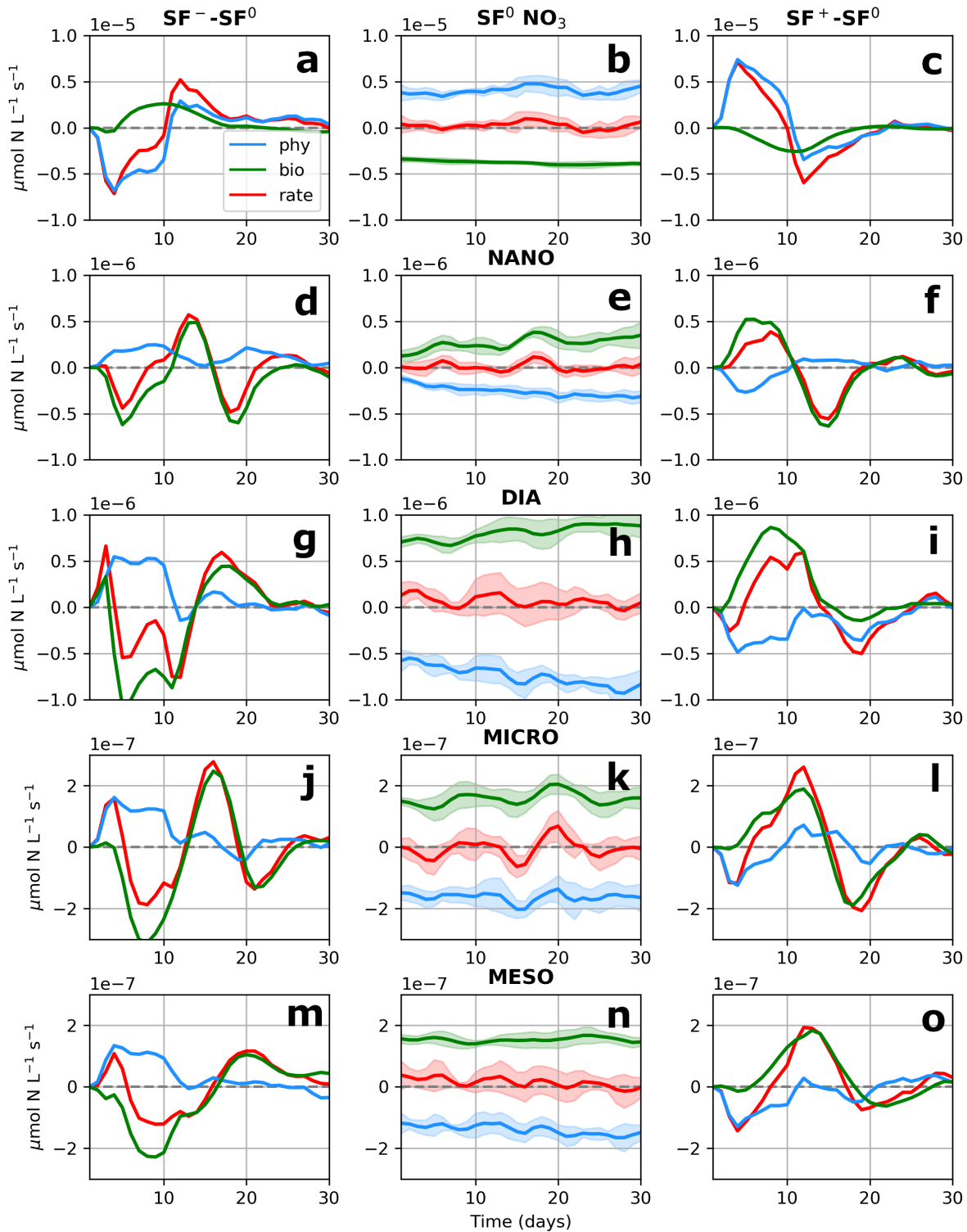


Figure 4: Time series of tendency terms of the biogeochemical tracer budgets (red line) along with their decomposition into a physical (blue lines) and biogeochemical (green lines) contribution. Spatial averaging is performed over the continental shelf ($h < 100\text{m}$) south of the Cape Verde peninsula (see green box in Fig.1a). The three columns represent the anomaly $\text{SF}^- - \text{SF}^0$ (left), the climatological simulations SF^0 (middle) and the anomaly $\text{SF}^+ - \text{SF}^0$ (right). The rows correspond (from top to bottom) to NO_3 , NANO, DIA, MICRO and MESO.

345 was presumably influenced by this process.

346 Moving up in the trophic chain, we turn to the implications of this change in nutrient stock and
347 enrichment rate for the plankton ecosystem. We start by noting that the magnitude of the perturbations
348 for the biological quantities was a moderate fraction of those for NO_3 . For example, the net NO_3 uptake
349 perturbation by the plankton ecosystem $\int F_{\text{NO}_3}^{\text{Bio}}(t) dt$ was $\sim 50\%$ of the total physical enrichment
350 perturbation between days 0 and 10 (the remainder $\sim 50\%$ was disposed of after day 10 by the physics -
351 see Fig. 4a,c). Likewise, biomass perturbations (in nitrogen units) were only a small fraction of the ones
352 for the nutrient stock (7-9% for phytoplankton; 2-3% for zooplankton).

353 Overall, the examination of \mathcal{W}^\pm for plankton abundance (Fig. 5) revealed a moderate attenuation of the
354 perturbation amplitudes from phytoplankton to zooplankton (*e.g.*, from $\mathcal{W}^\pm(\text{DIA}) \approx 30\%$ to
355 $\mathcal{W}^\pm(\text{MESO}) \approx 20\%$), with an exception for small planktons NANO and MICRO in SF^+ (see above
356 section 4.2 for our explanation invoking scrambling of trophic links by SF^+ intense ocean physics). A
357 large dispersion of the small plankton responses can be observed among the ensemble, contrasting with
358 the larger plankton boxes.

359 The attenuation of the perturbation as it propagated up the foodchain contrasted with the trophic
360 amplifications found in some previous studies (Chenillat et al., 2013; Kwiatkowski et al., 2019). This
361 was despite our biogeochemical model having a non predatory linear loss term for zooplankton, which is
362 known to favor trophic amplification, at least in equilibrium conditions (Kwiatkowski et al., 2019). Here
363 though, the duration of the nutrient input pulse/deficit (~ 10 days) was too short to let MESO reach
364 equilibration with the (transient) SF^\pm conditions (for example, note how NO_3 concentrations had already
365 nearly returned to climatology at day 15 when MESO was peaking; see Figs. 3c,g).

366 In summary, it thus appears that our relatively long synoptic events (by West African standards) were not
367 particularly apt at stimulating large plankton responses, particularly along the so-called short food chain
368 (nutrients to diatoms to copepods; (Kämpf & Chapman, 2016)).

369 **6 Discussion and conclusions**

370 *Modest impact of synoptic variability on the SSUS ecosystem*

371 Overall, our findings support the general idea that synoptic fluctuations produce modest disturbances in
372 a coastal upwelling sector like the SSUS. The propagation of our idealized synoptic perturbations in the
373 plankton model was characterized by: a large degree of relaxation-intensification symmetry (hence

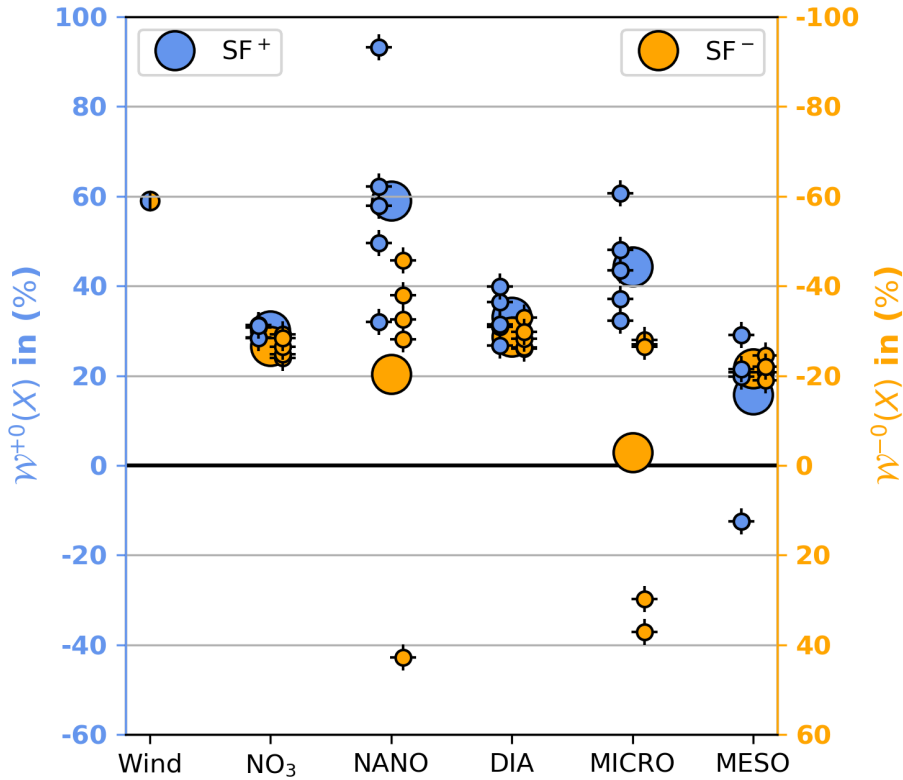


Figure 5: Magnitude $\mathcal{W}^{\pm 0}(X)$ of SF^+ (blue, left axis) and SF^- (orange, right axis) perturbations along biogeochemical and biological levels over the shelf south of Cape Verde peninsula ($h < 100m$, see Fig. 1a). Smaller dots indicate ensemble members, larger dots indicate ensemble averages. Note the large dispersion for the small plankton (NANO and MICRO) responses.

374 limited potential for net rectification associated with variability in this scale range); a mild trophic
375 attenuation; a low transfer efficiency of the synoptic nitrate perturbation into plankton biomass. All
376 these characteristics were a priori specific to the SSUS geomorphology and dynamical regime (and also
377 presumably dependent on our choice of model parameters).

378 Some of our findings may seem in apparent contradiction with existing evidence that synoptic
379 variability/intermittency plays an important role in the functioning of upwelling ecosystems, most
380 notably in sectors like ours where headlands and bays promote the existence of robust/frequent retentive
381 circulation features (Vander Woude et al., 2006). Specifically, the role of relaxation episodes found to be
382 essential in some sectors (Dugdale et al., 2006; Burger et al., 2020; Wilkerson et al., 2006) (Burger et al.,
383 2020) was not evidenced herein. Several comments are in order to help clarify this.

384 First, many of the studies supporting the view that synoptic variability is important are concerned with
385 the reproduction success of species with egg/larval planktonic stages and specific recruitment
386 requirements (Pfaff et al., 2015; Menge & Menge, 2013) such as the necessity to settle nearshore.

387 Typically, the success metrics demands that the scale of the organism's drift
388 $L_{drift} = \int_{t_0}^{t_0+T_{eco}} u(x(t), y(t), z(t)) dt$ be commensurate with the cross-shore width of the coastal habitat
389 suitable for the organism under consideration, where T_{eco} is the duration of the ecological process under
390 consideration (e.g., larval/planktonic life stage), u is the cross-shore horizontal current field, initial
391 release points $[x(t_0), y(t_0)]$ cover the coastal spawning areas, and $z(t)$ is determined by organism behavior.

392 The integral is computed along the Lagrangian trajectory followed by organisms. This framework is also
393 appropriate when considering the primary production available to the ecosystem of continental shelves
394 (Botsford et al., 2006). In sectors with strong climatological winds and/or a narrow continental shelf,
395 recruitment success can only be achieved intermittently when cross-shore transport compensations occur
396 thanks to variability of the velocity field in time, and/or in space (e.g, mesoscale turbulence). Synoptic
397 variability then produces temporal windows that, despite their shortness, are essential because they make
398 recruitment success non-zero. Note that wind synoptic variability can also help to meet recruitment
399 success requirements which call for limited alongshore displacements from spawning to recruitment,
400 when alongshore habitat heterogeneities exist due to the nature of the bottom substrate or prevailing
401 thermohaline conditions. In contrast to large parts of the Californian, Chilean, and South African
402 upwelling systems, the SSUS is characterized by a wide continental shelf and regional alongshore
403 pressure gradients that favor smaller L_{drift} values/longer coastal retention. This is, we think, the main
404 reason why the SSUS was only modestly sensitive to wind synoptic variability.

	P ⁺ / P ⁻	P ⁺ / P ⁻	P ⁺ / P ⁻
T _{avg} (days)	5	10	20
Occurrence	15 % / 9%	6% / 2.5%	6% / 2.5%
Perturbation (N m ⁻²)	±0.032	±0.032	±0.025

Table 1: Probability of exceeding a wind intensification/relaxation perturbation (P⁺/P⁻) threshold over a T_{avg}-long period during the upwelling season (December-May years 2000-2010). Wind perturbation statistics are computed by time-averaging a low-pass filtered time series of ERA5 wind stress in the box (-19°E, -16.5°E, 12.5°N, 15.5°N) over all possible T_{avg}-long time windows that start at 12PM (i.e., two consecutive windows overlap over T_{avg}-1 days). We use a Butterworth filter with a threshold period of 115 days for low-pass filtering. For each column, the row with the values in bold is the one deduced after having fixed the other two rows. Thus, for example, 20 day-long wind perturbations with a probability of occurrence similar to the one of the 10-day long SF[±] used in this study would have a magnitude of ±0.025 N m⁻², i.e. 25% less than SF[±]. Similar results were obtained with a threshold period of 60 days for low-pass filtering.

405 Second, although our choices for intensity and duration of the wind stress perturbations made our study
406 cases quite extreme (see section 2 and Table 1), we only considered one simple form of synoptic
407 disturbance. Compound events such as intensification-relaxation sequences would be interesting to
408 study. Longer events (*e.g.* ~20 days) would have a greater impact on plankton dynamics but, in a system
409 like the SSUS, the typical magnitude of the wind perturbation would be smaller (see Table 1). Running
410 simulations with a complex/realistic wind history will be useful to identify synoptic outlier events
411 (Jönsson & Salisbury, 2016). On the basis of (Thomsen et al., 2021), we presume that air-sea heat
412 exchanges cooling the ocean (more than in the present SF experiments) could substantially affect the
413 synoptic response of plankton.

414 Third, note that we have presented a shelf-wide view of synoptic effects while the response of the inner
415 shelf appeared stronger and more nonlinear in nutrients, NANO and MICRO (*e.g.* the SF⁺ perturbation
416 peak for NO₃ was nearly three times larger than over the entire shelf and thus larger than the atmospheric
417 perturbation amplitude, not shown). SF[±] asymmetries were also amplified over the inner shelf
418 considered in isolation, particularly for small plankton classes. The inner shelf planktonic ecosystem
419 may have been oversimplified in our simulations due to the absence of explicit cyanobacteria in our
420 model providing diatoms with ammonium in the surface layer (Bonnet et al., 2016) or sedimentary

421 sources of nutrients.

422 Finally, a representation of zooplankton involving several life stages (including dormance/diapause) and
423 diel vertical migration behavior would enhance the richness of and nonlinearities in physics-plankton
424 interactions and trophic coupling. Having some ontogenetic time scales in the synoptic range would
425 presumably magnify the effect of the latter in our system.

426 *Realism of the model synoptic behavior: Plankton concentration oscillations*

427 Whether biogeochemical models have appropriate functional forms to represent biological reactions, and
428 what implications model choices have on model behavior, are long-standing issues in biogeochemical
429 modeling (Hallam, 1978; Steele & Henderson, 1992; Franks, 2009), particularly with regard to the
430 tendency of models to produce (or not) predator-prey oscillations (Gentleman & Neuheimer, 2008). Our
431 simulations showed weak oscillations despite substantial perturbations in nitrate flux (Fig. 4). In its
432 design PISCES incorporates two standard stabilizing features: a 4 plankton group ecosystem connected
433 via multiple feeding pathways and a quadratic predation-type closure for zooplankton. It nevertheless
434 produced some manifestation of mild prey-predator interactions as a response to synoptic forcing
435 fluctuations and also in steady state following advection pathways emanating from the upwelling source.
436 Multi-year simulations with realistic forcings could reveal if the latter have a chance to be observed in
437 the real ocean. If so, two moorings with physics and biogeochemical sensors located over the transition
438 inner-to-mid shelf at two latitudes judiciously chosen could provide an interesting model evaluation and,
439 perhaps a way to make progress.

440 Furthermore, testable patterns of model synoptic responses could be uncovered for other upwelling
441 sectors, in particular where synoptic activity is consistently paced by intra-seasonal atmospheric modes
442 (as is the case in the southern hemisphere mid-latitude sectors, *e.g.* (Dewitte et al., 2011) in the Peru
443 upwelling system).

444 *Realism of the model synoptic behavior: Nanophytoplankton vs diatoms*

445 The fact that the planktonic response to synoptic events involved nanoplankton and diatoms in roughly
446 equal proportions (for example, both compartments captured similar amounts of the excess nutrients
447 associated with SF⁺) may seem at odds with what is known about plankton in upwelling systems and
448 more generally (Sommer et al., 2002; Ferreira et al., 2020; Ward et al., 2014). Model parameters could
449 be tuned differently so as to favor the diatom's response. Most simply, the NANO growth (resp.,
450 microzooplankton predation on NANO) rate could be diminished (resp. increased). However, this would

451 also decrease the mean NANO biomass which was a factor ~ 3 smaller than DIA biomass in our
452 simulations (Fig. 3), at odds with preliminary observation-based estimates (E. Machu, unpublished data)
453 Alternatively, we recognize that some of the physiological features susceptible to provide diatoms with a
454 competitive advantage were not included in PISCES: a faster response time to changing environmental
455 conditions (e.g, surge uptake and/or large nutrient stores (Fawcett & Ward, 2011; Lampe et al., 2021));
456 an ability to sustain high growth rates on NO_3 , e.g., due to lower metabolic cost or greater uptake
457 capacity (Marañón, 2015).

458 *A plea for coordinated modeling experiments across upwelling systems*

459 (Chabert et al., 2023) and the present study offer a reproducible framework that can be implemented in
460 or adapted to other upwelling sectors and other modelling systems (e.g., to explore sensitivity to
461 biogeochemical model parameterizations). We believe that this would provide new insight and research
462 avenues pertaining to the functioning of upwelling ecosystems. Such a synoptic "initiative" may not
463 provide direct answers to our most pressing science questions, which mainly concern longer time scales.
464 But as a trial run, it would generally contribute to advancing coastal plankton ecosystem models. Such
465 an initiative would also be timely, with the mounting impacts of (and interest in) extreme marine events,
466 many of which are in the synoptic scale range (Pietri et al., 2021), or intermittently aggravated/mitigated
467 and possibly initiated by synoptic events (Dalsin et al., 2023). Dissolved oxygen dynamics are also
468 strongly modulated on synoptic time scales (Machu et al., 2019; Tall et al., 2021; Adams et al., 2013;
469 Galán et al., 2020; Frieder et al., 2012), with potentially widespread consequences on higher trophic
470 levels. We provide a toolkit to facilitate the implementation of synoptic sensitivity frameworks similar to
471 ours in other systems (https://github.com/pierrechabert/toolkit_windevents). Ultimately,
472 our hope is that this will spawn a line of coordinated comparison studies across systems, exploring
473 synoptic scales and beyond.

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478 **Data Archiving**

479 Given the large size of the dataset (~ 2 TB), it is not stored online. The data can be made available upon
480 request to the authors.

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