

1 **Rapid Fluctuations of the Subsurface Chlorophyll**
2 **Maximum in Response to Wind Forcing in a Long,**
3 **Narrow Bay**

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10 **Key Points:**

- 11 • Upwelling events (~3 days) in the Galician Rías Baixas are enhanced by the com-
12 bination of shelf and local winds.
- 13 • Phytoplankton grow rapidly (1-3 days) within the upwelled nutrient-rich isopy-
14 cnals when they are transiently exposed to light in the rías
- 15 • Short-lived phytoplankton blooms are controlled by the rapid, adiabatic and re-
16 versible upwelling of deep isopycnals.

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Abstract

17 Bays within eastern boundary upwelling systems (EBUS) are ecological hot-spots fea-
18 turing a diverse range of spatio-temporal dynamics. At the EBUSs' poleward limit, up-
19 welling occurs in short-lived (<1 week) pulses modulated by synoptic wind variability.
20 The circulations in long, narrow bays can respond to these fluctuations within few hours.
21 The short-term biological response to these pulses was investigated in two of these bays
22 (Rías Baixas, NW-Iberia) with a two-week quasi-synoptic spatio-temporal survey in the
23 summer 2018. A four-day-long upwelling pulse caused deep, nutrient-rich isopycnals to
24 rise into the euphotic zone inside the bays, triggering a rapid (~ 1.7 days) nutrient up-
25 take and formation of a subsurface chlorophyll maximum (~ 3.8 days). The phytoplank-
26 ton biomass was transported rapidly toward deep, offshore waters when the winds weak-
27 ened. These results suggest that high productivity in narrow bays is controlled by the
28 transient exposure of deep, nutrient-rich waters to light during upwelling pulses.
29

Plain Language Summary

31 Equatorward winds off the main west continental coasts are responsible of the up-
32 welling of deep, nutrient-rich waters to the surface. For this reason, eastern boundary
33 upwelling systems (EBUS) are the most productive areas in the world's oceans. Bays within
34 EBUS are ecological hot-spots that provide food and protection for a myriad of organ-
35 isms. The circulation in long, narrow bays reacts very rapidly to short-lived upwelling
36 pulses (~ 3 days) related to weather patterns. In this study, we used high-resolution ob-
37 servations in two upwelling bays (Rías Baixas, NW Iberian Peninsula) to study how phy-
38 toplankton –the microalgae that sustain the ecosystem– respond to short-lived wind pulses.
39 During a 17-day cruise, we documented a four-day-long southward upwelling-favorable
40 wind event causing deep, nutrient-rich water to rise into the well-lit zone inside the bays.
41 Phytoplankton rapidly uptook nutrients and grew within the upwelled waters, trigger-
42 ing the formation of an intense bloom. The bloom was then transported toward deep,
43 offshore waters when the winds weakened. Our findings suggest that the extraordinary
44 productivity of narrow, upwelling bays is underpinned by the rapid response of the plank-
45 ton communities to the succession of intermittent short-lived upwelling events.

1 Introduction

Eastern boundary upwelling systems (EBUS) are among the most productive ocean ecosystems, supporting 10% of oceanic new production (Fréon et al., 2009), despite covering only $\sim 1\%$ of the global ocean's surface. The extraordinary biological productivity of these systems is driven by their hydrodynamics – in particular, their response to wind forcing. Equatorward winds drive Ekman transports that displace surface waters from the coast to the open ocean, resulting in the uplift of deep, nutrient-rich waters towards the euphotic zone. Bays located within EBUS can be even more productive than offshore waters, acting as hot-spots for phytoplankton growth. Due to their shape, bays can have long residence times of high-nutrient upwelled waters, providing retention zones with enhanced phytoplankton growth (Largier, 2020). These bays can thus support intense fishing and shellfish production through aquaculture (Trainer et al., 2010). Despite the common driving forces, EBUS are highly heterogeneous, presenting a diverse range of spatio-temporal dynamics depending on local bathymetry and the spatio-temporal variability of the wind forcing (Arístegui et al., 2009; Chavez & Messié, 2009). As localized upwelling hot-spots, bays within EBUS display a particularly rich suite of dynamical and ecosystem responses (Largier, 2020), which have profound implications for the communities relying on them as a source of food and services.

The Galician Rías Baixas are four long, narrow bays located at the northern limit of the Canary Current eastern boundary; here coastal upwelling supports a highly productive food chain and one of the most economically important marine industries in Europe (Blanton et al., 1987; Figueiras et al., 2002). Due to their latitudes, the temporal dynamics of upwelling in the rías are governed by synoptic-scale wind variability, which displays a strong seasonal modulation (Wooster et al., 1976). Southward, upwelling-favorable winds prevail between April and October, and northward downwelling-favorable winds from October to March (Wooster et al., 1976). As a consequence of fluctuating synoptic forcing, upwelling in these bays is not a steady process resulting from the large-scale equilibrium between the wind stress, the Coriolis force, and baroclinic pressure gradient, as in the classical formulations (Bowden, 1983). Instead, upwelling occurs as a series of transient events with a typical duration of ~ 3.3 days, interspersed with relaxation or downwelling events (Gilcoto et al., 2017).

The circulation of the rías responds to changes in the wind forcing (Cordeiro et al., 2021) within ~ 6 hours (Gilcoto et al., 2017). This is considerably faster than expected in a classical coastal upwelling system, where the shortest time scales relate to the rotational spin-up of the Ekman surface layer (Allen, 1973): the inertial period (17.85 hours at 42.23° N). The fast response in the rías results from the combination of shelf and local winds, and the shape and dynamical characteristics of the rías. Local winds are funneled along the bays by the local topography, such that upwelling-favorable (respectively downwelling-favorable) winds over the shelf occur synchronously with down-bay (resp. up-bay) winds (Herrera et al., 2005; Gilcoto et al., 2017). Because the rías are relatively narrow and deep (deeper than the Ekman depth), the fast initial response to wind forcing occurs through an along-bay momentum balance involving the wind stress, the barotropic pressure gradient, and friction (note: not Coriolis) (Lentz & Fewings, 2012). This results in a rapid, linear spin-up of the exchange flow in response to upwelling/downwelling winds (see Supplementary Text 1). After the initial spin-up, the exchange flow is subsequently reinforced by the coupling of the slower rotational local (ría) and shelf responses (Souto et al., 2003; Barton et al., 2015; Gilcoto et al., 2017).

Recently, a combination of highly resolved observations in space (Barton et al., 2015) and time (Barton et al., 2016; Gilcoto et al., 2017; Fernández-Castro et al., 2018), with regional models (Souto et al., 2003; Cordeiro et al., 2021), has substantially increased our understanding of the hydrodynamical responses of the Rías Baixas to transient upwelling/downwelling pulses, however, due to a prior lack of fine-scale biochemical data, we do not have a detailed characterization of the ecosystem response to these dynamics in these rías. Thus, while plankton growth dynamics in the region are intrinsically linked to

99 high-frequency variability of the wind-driven circulation, they have been historically inter-
 100 preted in terms of the seasonal variations of meteorological and environmental conditions
 101 (Nogueira et al., 1997; Nogueira & Figueiras, 2005; Díaz et al., 2016; Cermeño et al., 2006).
 102 Here we investigate the coupling between the high-frequency upwelling dynamics and plank-
 103 ton growth using data from a spatially extensive, temporally intensive survey around the
 104 two southern-most Rías Baixas (Ría de Vigo and Ría de Pontevedra) during the summer of
 105 2018.

106 2 Materials and Methods

107 The REMEDIOS-TLP cruise was carried out between 29 June and 16 July 2018 in the
 108 northwest of the Iberian Peninsula, specifically in two long narrow bays (Ría de Pontevedra,
 109 north, and Ría de Vigo, south), and the adjacent shelf (Fig. 1c). The sampling area is
 110 located at the northern end of the Canary Current-Iberian Upwelling System where the
 111 regional circulation is affected by cycles of wind-driven upwelling and downwelling (Fraga,
 112 1981). The mean water depth in the sampling domain ranged from 15 to 60 m between the
 113 inner and outer parts of the bays, dropping sharply at their mouth to ~ 115 m deep at the
 114 westernmost sampling points over the shelf break (see Supplementary Figure S4).

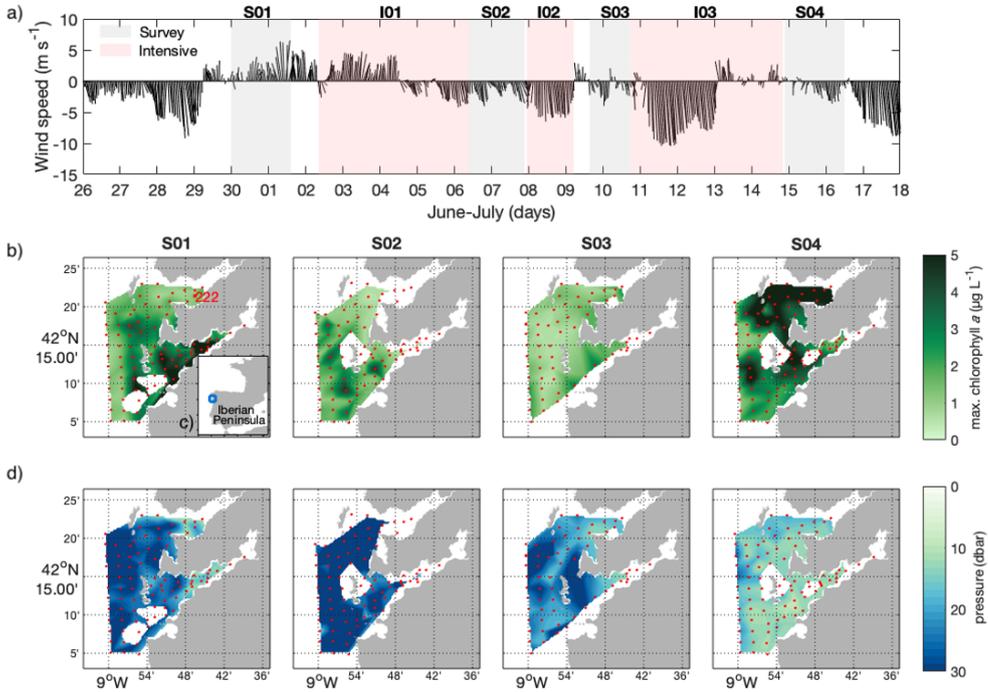


Figure 1. a) Time series of shelf winds throughout the cruise. Negative (positive) values correspond to upwelling (downwelling) favorable winds, mainly southward (northward) winds. Grey shaded areas show the survey sampling periods S01-S04, whereas the red areas indicate the intensive samplings I01-I03. b) Maximum chlorophyll *a* within the isopycnal range $\sigma_t = 26.4-27 \text{ kg m}^{-3}$. The first map shows the location of the intensive station, 222. c) Study area location within the Iberian Peninsula. d) Pressure at the maximum chlorophyll *a* concentration, within the same isopycnal range as b. Red dots in b and d correspond to the stations sampled in each survey.

115 A grid of 84 stations throughout the area (Fig. 1b) was sampled during four surveys on
 116 board of R/V Ramón Margalef: S01 (29 June to 01 July), S02 (6-7 July), S03 (9-10 July)
 117 and S04 (14-16 July). The survey samplings were interspersed by three periods of intensive
 118 sampling at a fixed station inside the Ría de Pontevedra (station 222, ~ 30 m, 42.35°N ,
 119 8.77°W): I01 (02-06 July), I02 (07-09 July) and I03 (10-14 July).

120 During the survey samplings (S01-S04), a SBE911 conductivity-temperature-depth
 121 (CTD) profile was acquired at each station. The SBE911 was equipped with fluorescence
 122 and photosynthetically active radiation (PAR)t sensors.

123 During the intensive samplings (I01-I03), CTD profiles were recorded with a MSS90
 124 microstructure profiler (Prandke & Stips, 1998) equipped among others with a fluorescence
 125 sensor. Five casts were performed every half hour, gathering a total of 1675 profiles over the
 126 three intensive samplings. These continuous measurements were paused every six hours (8
 127 am, 2 pm, 8 pm, 2 am) to conduct water collection at 7-8 depths with a rosette equipped with
 128 12 Niskin bottles, for determination of inorganic nutrients and chlorophyll concentrations.
 129 These chlorophyll samples, as well as other samples collected during the seasonal samplings
 130 of the REMEDIOS project (March 2017 to May 2018) were used to calibrate the MSS90
 131 fluorescence sensor ($n = 65$). The fitted calibration curve was:

$$\text{chlorophyll } a = 1.460 \times \text{fluorescence} - 0.248, (R^2 = 0.901) \quad (1)$$

132 To calibrate the fluorescence sensor of the SBE911, a set of chlorophyll samples collected
 133 during the cruise at different stations throughout the study area was used ($n = 71$):

$$\text{chlorophyll } a = 0.270 \times \text{fluorescence} - 0.051, (R^2 = 0.855) \quad (2)$$

134 To determine nitrate concentrations, samples were frozen *in situ* at -18°C and analysed
 135 on land with a Skalar San Plus segmented flux analyser.

136 Wind data spanning the REMEDIOS-TLP period were acquired from an oceanographic
 137 buoy at the shelf (42.12°N , 9.43°W) operated by Puertos del Estado (data available at
 138 www.puertos.es); whereas wind data near the intensive station were acquired from the me-
 139 teorological station located at Cabo Udra, Bueu (42.34°N , 8.82°W) operated by Meteogalicia
 140 (data available at meteogalicia.gal).

141 3 Results

142 Time series of shelf wind (Fig. 1a) showed a strong upwelling-favorable wind event
 143 before the cruise, which relaxed a few hours before the initial spatial survey (S01). The
 144 following days were characterized mainly by northward, downwelling-favorable winds un-
 145 til the middle of the first occupation of the intensive time-series station (I01), on 4 July.
 146 Subsequently, southward, upwelling-favorable winds increased to a maximum on 11-13 July,
 147 during I03. This increase was interrupted by two days of weak winds coinciding with S03,
 148 on 9-10 July. Finally, the last 3-4 days of the cruise, coinciding with S04, were dominated
 149 by upwelling relaxation.

150 The subsurface chlorophyll maximum tended to follow isopycnals, and was located
 151 between $\sigma_\theta = 26.4 - 27 \text{ kg m}^{-3}$ during the study (Fig. 1b and 1d). During the field
 152 campaign, these isopycnals fluctuated up and down, and in and out of the rías depending
 153 on the upwelling-relaxation-downwelling state. The first 3-day sampling survey, S01, was
 154 conducted a day after an upwelling event, and during a downwelling event. High maximum
 155 chlorophyll values of $(2.6 \pm 1.9 \mu\text{g L}^{-1})$ were detected over the whole area (Fig. 1b). In Ría de
 156 Vigo and over the shelf, the chlorophyll concentrations were greater than $5 \mu\text{g L}^{-1}$ at several
 157 stations. The mean depth of the isopycnal range containing the chlorophyll maximum was
 158 $26 \pm 8 \text{ m}$, deeper than the mean euphotic depth in the rías (10% incident light, mean depth
 159 $16 \pm 2 \text{ m}$), and deeper over the shelf and the mouth of the rías ($>20 \text{ m}$) than in their interior
 160 ($\sim 18 \text{ m}$). During S02, two days after a downwelling event, the chlorophyll maximum was
 161 weaker ($1.5 \pm 1.0 \mu\text{g L}^{-1}$), and deeper than during the S01 survey ($32 \pm 9 \text{ m}$). Moreover,
 162 the isopycnal range was not present in the inner part of the rías, presumably an effect of
 163 the wind-driven downwelling. The subsurface chlorophyll maximum was weakest during S03

164 $(1.2 \pm 0.6 \mu\text{g L}^{-1})$, but it was shoaling ($23 \pm 7 \text{ m}$ in the rías) following upwelling-favorable
 165 conditions during the preceding days. By survey S04, the deep chlorophyll maximum was
 166 located much shallower than during previous surveys ($15 \pm 4 \text{ m}$ in the rías), and had reached
 167 its highest concentrations ($3.3 \pm 1.8 \mu\text{g L}^{-1}$).

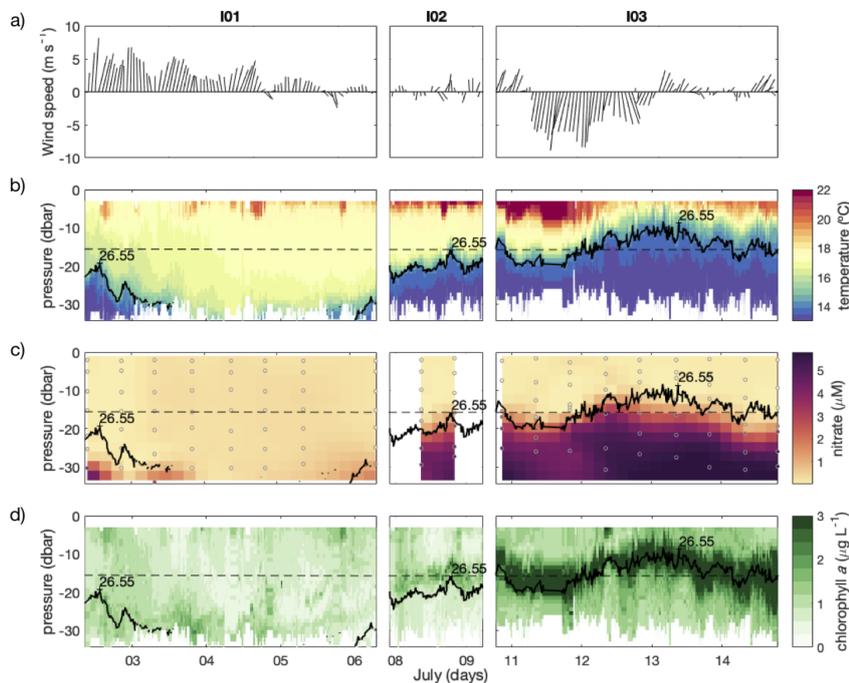


Figure 2. Time-series of a) wind, b) temperature, c) nitrate, and d) chlorophyll *a* during the occupations of the intensive station inside Ría de Pontevedra, 222. Black solid lines in panels b, c, and d represent the 26.4 kg m^{-3} isopycnal. Black dashed lines in panels b, c, and d represent the mean 10% incident light at intensive station, 222. Dots in panel c indicate when bottle samples were taken. In order to improve the representation, maximum of chlorophyll values was set to $3 \mu\text{g L}^{-1}$, thus values above $3 \mu\text{g L}^{-1}$ are not distinguished in panel d.

168 The intensive sampling time series at a single station in the ría, I01-I03, offer a higher-
 169 resolution temporal view of the chlorophyll dynamics inside the rías in response to variability
 170 in the wind forcing (Fig. 2b-d). In particular, large vertical fluctuations of the isopycnals
 171 containing the chlorophyll maximum are apparent at this station; these isopycnals showed
 172 at least a 25 m vertical excursion (close to the full depth range), closely coupled with the
 173 various upwelling-downwelling cycles. With the onset of downwelling-favorable winds at
 174 the beginning of I01, the chlorophyll-rich isopycnals (centered at 26.55 kg m^{-3}) deepened
 175 ($29 \pm 3 \text{ m}$), and showed only weak chlorophyll-maximum values ($1.0 \pm 0.3 \mu\text{g L}^{-1}$). Toward
 176 the end of I01, winds shifted to weakly upwelling-favorable and the 26.55 kg m^{-3} isopycnal
 177 shoaled (Fig. 2b). Nitrate levels were very low, exceeding $1 \mu\text{M}$ only below the chlorophyll
 178 maximum when those isopycnals were present (Fig. 2b-d). The next intensive sampling, I02,
 179 occurred after several days of weakly upwelling-favorable winds. During I02, the isopycnals
 180 containing the chlorophyll maximum shoaled, raising the chlorophyll maximum up to $20 \pm 2 \text{ m}$
 181 depth; maximum chlorophyll values were still low ($0.8 \pm 0.3 \mu\text{g L}^{-1}$). During I03, after two
 182 days of relaxation when the nutrient-rich isopycnals deepened slightly, a period of sustained,
 183 intense upwelling caused the isopycnals to rapidly shoal further to $< 10 \text{ m}$, well within the
 184 euphotic zone. The shoaling isopycnals were accompanied by the upward movement of
 185 nutrient-rich water into the base of the euphotic zone. During this time the chlorophyll
 186 values increased to their highest values during the study ($> 5 \mu\text{g L}^{-1}$).

4 Discussion

The different samplings developed during the cruise can be re-sorted in time (Fig. 3) to illustrate the response of the deep chlorophyll maximum to a typical wind-driven upwelling cycle. Before the intensification of southward, upwelling-favorable winds, (as encountered during I01 and S02), nutrient-rich isopycnals contain low chlorophyll and are found deep (> 30 m) in waters over the shelf; they are not present in the shallow (< 25 m) middle-inner part of the bays. When the wind starts blowing from the north (upwelling favorable), a circulation develops inside the bays driving the surface layer offshore, causing the deep isopycnals to rapidly shoal in the inner part of the rías. This shoaling brings deep, nutrient-rich water up to the base of the euphotic zone, allowing an increase of subsurface chlorophyll concentrations there, as in I02 and S03. During this upwelling in the rías, the isopycnals are still deep at the mouth of the ría, and over the shelf. If the upwelling-favorable wind continues, the nutrient-rich isopycnals are also advected upward into the euphotic zone over the shelf. At this point the bloom is in its most intense and widespread phase, with highest chlorophyll values found inside the bays where the isopycnals are shallower (e.g., I03 and S04). Finally, the wind relaxes or reverses to downwelling-favorable, causing the dense, chlorophyll-containing isopycnals to deepen and flow back offshore from the rías. As the chlorophyll-maximum layer deepens below the euphotic zone, the chlorophyll concentrations decrease, as found during S01.

The intensive sampling I03 showcases the rapid biological response to wind-driven fluctuations of isopycnals. At the beginning of this sampling, at 6 pm on 10 July, chlorophyll levels were high, but relatively deep (~ 17 m) due to the preceding upwelling/relaxation conditions (Fig. 3d). Upwelling-favorable winds started blowing at 4 am, on 11 July. Almost synchronously, the chlorophyll maximum layer reverted its deepening trend and began to shoal until 5 pm on 12 July. The layer remained stable above 10 m for 21 hours (Fig. 3c). The shoaling of the 26.55 kg m^{-3} isopycnal was immediately followed by a reduction of the nitrate concentrations (Fig. 2c, 3b) and an increase in chlorophyll concentrations (Fig. 2d, 3c). This is consistent with the phytoplankton on these nutrient-rich isopycnals being exposed to light, and responding by rapidly taking up nutrients, with subsequent accumulation of biomass. This enhanced phytoplankton growth is locally restricted to the deep, nutrient-rich waters when they are exposed to light. The isolation of these isopycnals from the surface shows that diapycnal mixing of nutrients into surface waters – a much slower process than upward advection of isopycnals – plays a secondary role in the rapid development of the bloom.

The time scales of the phytoplankton response during I03 can be computed as the e-folding times of nitrate uptake ($\tau_{NO_3^-} = 1.74$ d, Fig. 4a) and chlorophyll accumulation ($\tau_p = 3.80$ d, Fig. 4b) in the isopycnal range of the chlorophyll maximum. The wind decorrelation time scale of 3.2 d, computed for the complete upwelling season of 2018 (Fig. 4c), represents the duration of a typical upwelling event (Gilcoto et al., 2017). The biological time scales are thus comparable to or shorter than the duration of an upwelling cycle, allowing the biomass of phytoplankton to show an exponential increase over the course of an upwelling cycle.

Our observations thus show that phytoplankton can respond rapidly to the transient exposure of deep, nutrient-rich isopycnals to light, resulting in significant nutrient uptake and subsequent bloom formation, in spite of the short duration of wind-driven upwelling pulses (~ 3 days). The coupling between the time scales of wind forcing and phytoplankton growth could therefore explain the high phytoplankton primary productivity of the rías in the region (Aristegui et al., 2009). Further, the succession of synoptic-scale upwelling events ensures that high average primary productivity is maintained throughout the summer season despite the flushing of biomass offshore after the cessation of upwelling-favorable winds.

This bio-physical coupling is intensified by the rapid response of the isopycnal depths in the rías to changes in wind forcing – much faster than the Ekman spin-up time. The long

239 and narrow ($<$ baroclinic Rossby radius of deformation) morphometry of the rías (Largier,
 240 2020) means that the Coriolis force plays a secondary role in setting up the circulation
 241 patterns. Instead, the initial spin-up of the ría's circulation is a non-rotational response to
 242 the local – rather than shelf – winds (Gilcoto et al., 2017) (see also Supplementary Text 1).
 243 Furthermore, the mountains surrounding the bays channel the remote and mostly meridional
 244 winds in the along-bay direction, driving the surface water layer downwind (Gilcoto et al.,
 245 2017) to create rapid upwelling and downwelling in the rías.

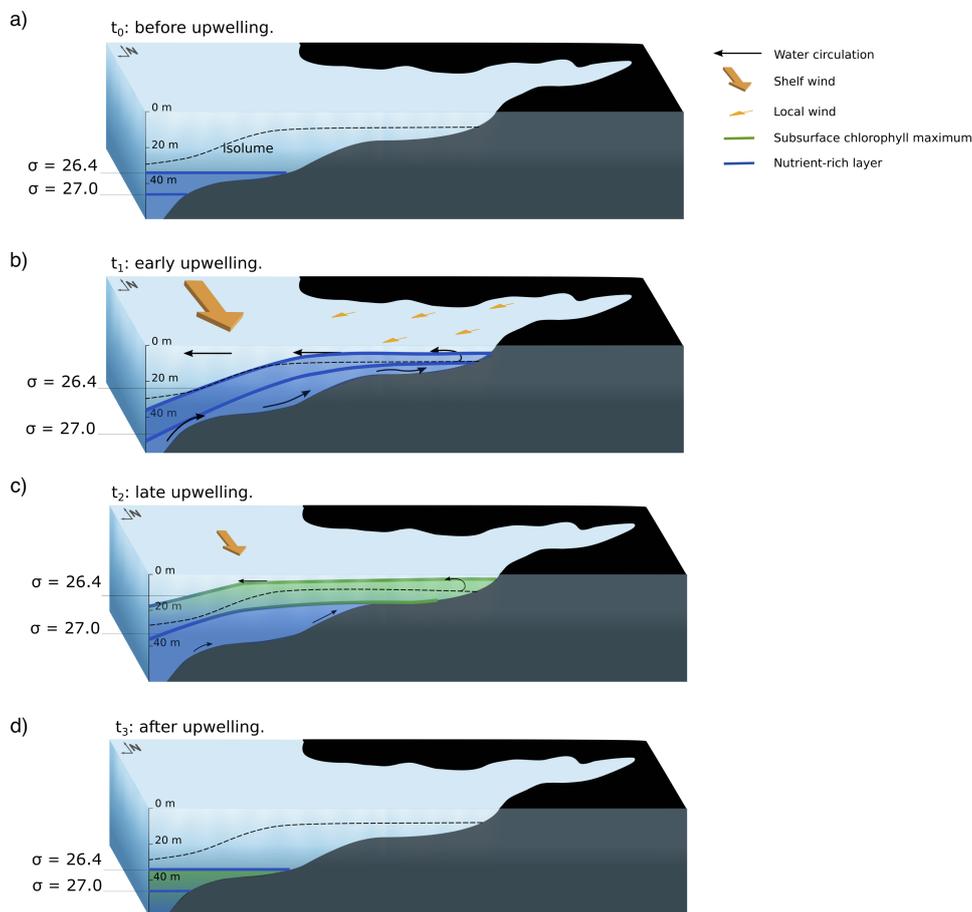


Figure 3. 3D schematics of a wind-driven upwelling cycle. a) Before upwelling: nutrient-rich isopycnals ($\sigma_t = 26.4 - 27 \text{ kg m}^{-3}$) are deep (I01 and S02). b) Early upwelling: wind stress forces surface waters down the bay. As a consequence, the isopycnals shoal into the euphotic zone inside the bays (I02 and S03). c) Late upwelling: high chlorophyll biomass forms when the nutrient-rich isopycnals are exposed to the light in the whole area (I03 and S04). d) After upwelling: as wind stops or reverses, the isopycnals deepen, carrying the high phytoplankton biomass with it (S01).

246 These rapid, wind-driven fluctuations of the pycnocline may also occur in other wind-
 247 forced bays that share the morphometric characteristics of the Galician rías. For example,
 248 Concepción bay (Chile), located in the Humboldt EBUS, is also classified as an elongated bay
 249 (Largier, 2020) and is oriented in the direction of the wind field during upwelling (northward
 250 winds), but partially sheltered from upwelling transport due to its south-to-north alignment.
 251 Though we do not have data from Concepción Bay, Daneri et al. (2012) and Peterson et al.
 252 (1988) studied Coliumo Bay, which is smaller, but adjacent to Concepción bay, and with a
 253 similar orientation. Transient upwelling events driven by synoptic wind forcing modulate
 254 the high primary productivity of this area (Daneri et al., 2012). Both studies (Daneri et
 255 al., 2012; Peterson et al., 1988) showed a lag time between wind stress and hydrographic

256 fluctuations of about 1 day, which is consistent with the local inertial period (~ 20 h).
 257 However, owing to their daily sampling interval, it is not possible to know whether more
 258 rapid hydrographic fluctuations were occurring; we would predict changes on an hourly time
 259 scale due to the similarity of this bay to our system.

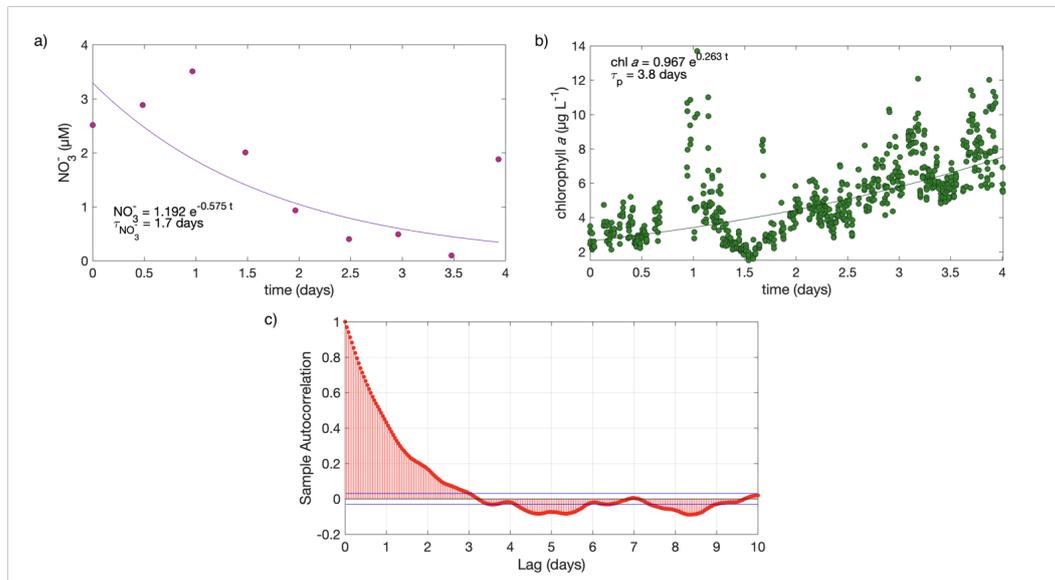


Figure 4. Exponential fits of a) nitrate and b) chlorophyll vs. time at $\sigma_\theta = 26.55 \text{ kg m}^{-3}$ during I03. Fitted equations and e-folding times for chlorophyll (τ_p) and nitrate ($\tau_{NO_3^-}$) are shown. c) 10 days of the autocorrelation function and 95% confidence intervals (blue lines) for along-shore wind from the full 2018 upwelling season time series (15 April to 15 October).

260 Another elongated bay, Dakhla Bay, located in the Canary Current EBUS (Largier,
 261 2020) is one of the most productive areas in Morocco in terms of shellfish farming (Zidane
 262 et al., 2008). It is also oriented NE to SW, as our bays, and the typical winds in the region
 263 are mainly from north and north-east (Zidane et al., 2008; Van Camp et al., 1991). This bay
 264 fits all the requirements to have rapid fluctuations of the subsurface chlorophyll maximum
 265 in response to both local and shelf wind forcing. However, no high-temporal-resolution
 266 samplings have been carried out here so far.

267 Our results have implications for mussel farming – the most productive marine aqua-
 268 culturing activity in the region (Labarta & Fernández-Reiriz, 2019). Mussels are cultured
 269 on 12-m long ropes hanging from rafts. The intermittent presence of nutrient-rich water
 270 near the surface is likely to affect mussel food supply and growth. Local mussel farmers
 271 report that the growth of mussels located near the surface is twice the growth of mussels
 272 deeper down on the ropes. However, they also point out that the deepest end of the rope
 273 (10 to 12 m) often has much larger mussels as well. These deep mussels are likely accessing
 274 the subsurface nutrient-rich, high-phytoplankton-biomass layer observed during upwelling
 275 conditions in our cruise. It is possible that longer ropes – with more frequent access to this
 276 layer – could benefit the mussel culture.

277 Every year, mussel harvesting is threatened by the presence of harmful algae blooms.
 278 Often, these harmful blooms appear related to the presence of thin chlorophyll layers
 279 (Broullón et al., 2020). However, traditional monitoring programs using either oceanog-
 280 raphic bottle samples taken at specific depth intervals or vertically integrated hose samples
 281 (Escalera et al., 2012; McManus et al., 2008; Velo-Suárez et al., 2008) may not adequately
 282 sample such layers. The dynamics of thin layer formation and their connections to harm-
 283 ful blooms remain poorly understood in this region, which hampers our ability to predict
 284 their occurrence, or offer useful advice to mussel farmers. In contrast, the high-resolution
 285 chlorophyll observations reported here showed the development of a subsurface chlorophyll

286 maximum which, at least during part of intensive sampling I03, had the characteristics of a
 287 thin layer (< 3 m thick). This finding underscores the need for highly spatially and tempo-
 288 rally resolved observations to better understand the biophysical processes involved in thin
 289 layer formation and their connections to harmful blooms.

290 5 Conclusions

291 The aim of this study was to investigate the coupling between phytoplankton growth
 292 and upwelling dynamics in two long, narrow bays (Ría de Vigo and Ría de Pontevedra, NW
 293 Spain) using a highly temporally and spatially resolved dataset collected during the 3-week
 294 REMEDIOS-TLP cruise (July 2018). Our results show that the long, narrow bay led to a
 295 rapid response of the along-bay circulation to along-bay winds – much faster than the inertial
 296 response found offshore. Short (~ 3 day) upwelling-favorable wind events caused isopycnals
 297 to rapidly shoal in the bay, exposing deep, nutrient-rich isopycnals to light. Phytoplankton
 298 on these deep isopycnals quickly (~ 2 days) took up nutrients, and increased in biomass
 299 (~ 3 days). This enhanced phytoplankton biomass fluctuated with wind-driven fluctuations
 300 of the isopycnal depths, and was advected into and out of the bays depending on the
 301 wind stress. Our data show that such short-lived phytoplankton blooms in these bays are
 302 controlled by the rapid, adiabatic and reversible upwelling of deep isopycnals, rather than
 303 the fertilization of surface waters by diapycnal turbulent mixing. It is therefore likely that
 304 these short-time-scale blooms explain the overall elevated biological productivity of such
 305 bays. Similar bio-physical coupling dynamics may drive high primary productivity in other
 306 upwelling bays that have comparable morphologies and orientations; these dynamics will
 307 only be revealed through highly spatially and temporally resolved surveys, such as those
 308 presented in this study.

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 319 Bathymetry data used in the Supplementary Information was obtained from GEBCO Com-
 320 pilation Group (2020) GEBCO 2020 Grid (<https://doi.org/10.5285/a29c5465-b138-234d-e053-6c86abc040b9>).
 321 Data sets for used in this research are available in Mendeley Data
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