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Cross-shelf variability in the Iberian Peninsula Upwelling System: impact of a mesoscale filament.

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Abstract

Based on a multidisciplinary survey in the Iberian upwelling during late summer 2007, this paper analysed comparatively the cross-shore variability and offshore transport across the upwelling front and within a mesoscale filament.

Along the East-West (EW) sections, transient upwelling pulses bring regularly cold, fresh and nutrient-enriched waters to the surface, triggering intense biological responses. Offshore advection by wind-forced Ekman drift of the successive fronts, interrupted by relaxation periods, drive the variability of the planktonic communities. While the near-shore areas are dominated by relatively small phytoplankton controlled by mesozooplankton grazing, large cells of diatoms appear after a short decay. While the microphytoplankton dominates largely the shelf communities, the species composition varies along the offshore drift with the apparition of dinoflagel-

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lates and the development of large zooplankton individuals. The oligotrophic ecosystem characterized by small organisms and low biomass (~ 80 km offshore) contrasts strongly with the transitional area and the coastal upwelling.

The low density waters within the filament and the existence of a pair of opposite rotating eddies at its base and tip promote its generation and rapid seaward extension. The intensified offshore advection of coastal enriched waters considerably increases the area favouring a productive ecosystem (until ~ 160 km off the coast). Cross-shelf variability of bio-physical variables is observed in the filament as along EW sections, although a subsequent homogenization within the mesoscale structure erases the sharp fronts. Off the shelf within the filament, the chlorophyll a is distinctly organised as a shallow subsurface maximum dominated by nanophytoplankton. The relative physical isolation of a dynamical food-web in the filament is also promoting nutrient remineralisation under the structure.

Finally, we estimate that mesoscale filaments, although being less extended meridionally than the upwelling front itself ($\sim 40 \%$ of the length of the front) are responsible of a greater offshore transport of chlorophyll ($\sim 60 \%$ of total cross-shelf exchanges) over the Iberian system. Despite the favourable wind pulses advecting westward the successive upwelling fronts, self-propelled filaments provide permanent offshore transport, even under wind relaxation period, thus playing a major role in cross-shelf exchanges.

Key words: Iberian Peninsula Upwelling, Cross-shore variability, Upwelling front, Mesoscale Filament, Biogeochemistry, Planktonic community

Abbreviations.¹

¹Eastern Boundary Upwelling Systems = EBUS; Iberian Peninsula Upwelling System = IPUS; Western Iberian Buoyant Plume = WIBP; Portugal Current = PC; Portugal Coastal Current

1 1. Introduction

Coastal upwelling systems are characterized by high productivity of plankton 2 and pelagic fishes, thus having a major biological and socio-economical role (Pauly 3 and Christensen, 1995). Their positive effect is not only restricted to the continen-4 tal margins where they occur, but it is also exported toward the adjacent oceanic 5 gyre. Indeed, coastal upwellings exchange water and biogeochemical properties with 6 the offshore regions through the complex and highly dynamical Coastal Transition Zones, the core of many multidisciplinary studies in the last two decades (Brink 8 and Cowles, 1991; Barton et al., 1998; Fréon et al., 2009). It has been shown that mesoscale processes such as filaments and eddies are ubiquituous features of these 10 transitional areas, in relation with the complex coastal circulation and bathymetry. 11 These structures promote an intense transport from the productive shelf region to-12 ward the oligotrophic gyre, thus fueling the open ocean with coastal biogeochemical 13 materials, including organic matter. Although it is difficult to precisely quantify 14 those cross-shelf processes, a review by Arístegui et al. (2009) suggests they have an 15 important role in the metabolic balance of the whole North Atlantic gyre. 16

This study is based on the MOUTON07 field experiment (Rossi, 2010) that took place in the Iberian Peninsula Upwelling System (IPUS). Although disconnected by the Gibraltar Strait, the IPUS is often associated to one of the four main winddriven Eastern Boundary Upwelling Systems (EBUS), the Canary-Iberian upwelling (Arístegui et al., 2009). However, an important difference between the Canary and

⁼ PCC ; Iberian Poleward Current = IPC; SCM = Subsurface Chlorophyll Maximum; PP = Primary Production; AOU = Apparent Oxygen Utilization; ESD = Equivalent Spherical Diameter; ENACWsp-st = Eastern North Atlantic Central Water of Subpolar/Subtropical origins.

Iberian areas is their temporal variability: the Canary region sees quasi-constant 22 trade winds which favour upwelling all year round, whereas the IPUS shows a strong 23 seasonality mainly due to the annual cycle of the atmospheric system. A winter 24 regime and a summer-fall regime are observed, with superimposed smaller scales 25 variability. During winter / early spring, weak equatorward winds occur transiently 26 and are associated with localized upwelling and moderate response from the well-27 mixed waters (Castro et al., 2000). During late spring / summer / autumn when the 28 stratification of the coastal ocean increases, a sustained along-shore southward wind 20 stress generates a strong upwelling (Fiuza et al., 1982) of cold nutrients enriched 30 waters at the coast, associated with an increase up to 50 % of the total primary 31 production (Joint et al., 2002). 32

During the favourable upwelling season, the physical circulation is complex and 33 is composed of large scale currents interacting with numerous and intense meso-scale 34 features (Relvas et al., 2007). The Portugal Current (PC), a south-west surface drift 35 offshore, is established and is usually associated with a coastal jet flowing equa-36 torward (Peliz et al., 2002), the Portugal Coastal Current (PCC). In addition, a 37 poleward slope counter-current, named the Iberian Poleward Current (IPC), is ob-38 served at many periods of the year but intensified in non-upwelling season, i.e. winter 30 (Peliz et al., 2005). 40

A quasi-meridional upwelling front develops between the cold recently upwelled enriched waters at the coast and warmer oligotrophic offshore waters. This strong cross-shore temperature gradient, itself related to the ambient nutrient concentrations, is indeed strongly influencing the phytoplankton assemblages (Resende et al., 2007). Tilstone et al. (2003) and Lorenzo et al. (2005) also described the coastal upwelling communities as microplankton dominated, whereas mainly cyanobacteria (picoplankton) are found in the oceanic waters.

Due to small scales instabilities (Relvas et al., 2007), mesoscale processes such as 48 filaments and eddies are commonly observed along the upwelling front, i.e. occurring 49 mainly from July to October (upwelling season). Large filaments were often closely 50 related with capes and coast irregularities, but the repeated occurrence of a few large 51 filaments at different locations corresponding with a straight coastline have also been 52 noted. Different processes have been studied (Haynes et al., 1993; Roed and Shi, 1999; 53 Batteen et al., 2007; Sanchez et al.) and among others, the capes effect, front and 54 flow instabilities resulting in meander formation, and lately the creation of vorticity 55 anomalies by upwelling current/topography interactions (Meunier et al., 2010) can 56 be cited. 57

Other authors focused on the biological role of these filamental structures. Alvarez-58 Salgado et al. (2001, 2007) showed they are responsible for important cross-shelf ex-59 change of biological material while seeding the oligotrophic offshore waters with nutri-60 ents and organic materials. Filaments also constitute ecological niches by themselves, 61 where changes in biological process rates (Alvarez-Salgado et al., 2001; Fileman and 62 Burkill, 2001), phytoplankton (Joint et al., 2001) and zooplankton populations (Bat-63 ten et al., 2001; Halvorsen et al., 2001) occur within the structure during its offshore 64 drift. In addition, Borges and Frankignoulle (2001) claimed that upwelling filaments 65 are partly controlling the partial pressure of CO_2 in the area, thus playing a key 66 role in the inorganic carbon cycle and the ocean acidity regulation. More recently, 67 (Cravo et al., 2010) studied an upwelling filament off south west Iberia and found 68 that it carried large amount of chlorophyll a as well as nutrient offshore the coastal 69 upwelling front. A review of the existing bibliography in the north Atlantic showed 70 that although variable, large amounts of nutrients, gases and plankton are exported 71 toward the open ocean through these structures (Arístegui et al., 2009; Cravo et al., 72 2010). 73

Overall, although the seasonality of the Iberian upwelling is linked with synoptic atmospheric systems, the system is also highly variable at smaller scale. During the upwelling season, a sharp meridional front is developing between the productive coastal waters and the oligotrophic open ocean, regularly interrupted by numerous filaments and eddies. The mesoscale variability of this transitional area, its influence on biogeochemical properties and planktonic communities, and its associated crossshelf export are still not properly quantified.

Based on a multidisciplinary data set collected over the central and northern IPUS during upwelling-favourable conditions in August-September 2007, the crossshore variability is investigated under two different situations. We compare two zonal sections through the sharp upwelling front at 40° and 41°N to a network of transects carried out within and across a filament.

After presenting the oceanographic context (sect. 3.1), we briefly described the shelf circulation in section 3.2. We then compare the physical structure of the successive upwelling fronts and of the filament extending offshore (sect. 3.3). It results in specific biogeochemical and biological cross-shore variability examined in sect. 3.4 and 3.5. Finally, we estimate the contribution of both structures to seaward fluxes of enriched coastal waters (sect. 3.6).

⁹² 2. Materials and methods.

⁹³ 2.1. The MOUTON 2007 survey: general information and sampling strategy.

The MOUTON07 cruise was conducted along the western coast of the Iberian Peninsula (mainly Portuguese coast), onboard the Research Vessel R/V "Pourquoi-Pas?". It aimed at studying the mesoscale variability both from a physical and ⁹⁷ biogeochemical point of view in the central and northern part of the IPUS during
⁹⁸ the upwelling-favourable season.

⁹⁹ The survey was divided in two legs, from August 14^{th} to August 25^{th} and then ¹⁰⁰ from August 30^{th} to September 9^{th} , 2007 (see Fig. 1).

To study the cross-shore variability of the IPUS, two zonal sections across the 101 quasi-meridional upwelling front and an intensive survey of a mesoscale filament were 102 carried out thanks to real-time acquisition of satellite data onboard. Both East-West 103 sections EW1 at 41°N and EW2 at 40°N started at around 10 km from the coast, 104 crossed the upwelling front and ended at about 100 km offshore (see Fig. 1). The 105 sampling was focused on a filament initiating at around $40.3^{\circ}N$, elongating offshore 106 almost zonally. A transect was first performed from the coast to ~ 200 km offshore 107 within the filament followed by several North-South transects across the structure 108 (see Fig. 1 and Fig. 7a). 109

110 2.2. Bio-physical sensors and water sampling.

Physical observations were made using a Conductivity-Temperature-Depth (CTD) 111 probe, a Lowered Acoustic Doppler Current Profiler (LADCP) functioning at 300 kHz, 112 and two Vessel Mounted Acoustic Doppler Current Profilers (VMADCP), function-113 ing at 38 kHz and 150 kHz, respectively. Meteorological and underway data were 114 simultaneously recorded from the sensors onboard the R/V. Sea surface winds de-115 rived from the QuikSCAT scatterometer (averaged over the surveyed area $39-43^{\circ}N$ 116 $/ 9 - 12^{\circ}$ W) are used when the onboard measurements were not available. Mean-117 while, a set of biogeochemical as well as optical sensors were also mounted onto the 118 CTD-rosette. In this paper, data from a fluorometer Chelsea Aqua 3 for chlorophyll 119 a and from an Oxygen sensor SBE43 lowered on the Rosette are presented. 120

¹²¹ More than a thousand CTD casts were carried out during the cruise (see Fig.

1), composed of around 430 casts using a "physical CTD-Rosette" system lowered 122 down to 2000 m at offshore locations and around 960 casts using a "biogeochemical 123 CTD-Rosette-Niskin" system limited to the upper 200 m (due to the maximum 124 operation depth of biogeochemical sensors). Among the "biogeochemical" stations, 125 seawater samples were collected at around 150 stations using the biogeochemical 126 rosette equipped with 12 ten litres Niskin bottles. In this paper, our analysis focus 127 on the "biogeochemical" stations that compose the cross-shelf transects EW1, EW2 128 and the filament network, while the whole dataset provide an overview of the local 129 oceanography down to 2000 m. 130

At each station, the downcast profiles of temperature and fluorescence were used to visually determine up to five depths in the water column, sampled during the upcast: the surface (1 m), the upper thermocline, the deep chlorophyll maximum, the lower thermocline and an additional depth of interest.

Error estimates are around 5 cm/s for all current sections presented here. Rough conditions occurred during the survey, especially during the leg 1, due to intense northerlies (see Fig. 2) and a large ground-swell (~ 3 m) which affected the ship navigation offshore as compared to the relatively protected shelf areas. As a consequence, the open ocean currents data (for depths greater than 200 m) are not analyzed in this paper.

The fluorometer (chlorophyll *a* probe) from the rosette was calibrated using chlorophyll *a* concentration in mg/m³ measured by HPLC (see Sec. 2.3.2). The values of total chlorophyll *a* are obtained by multiplying the corresponding fluorescence by a factor of 3 ($R^2 = 0.75$).

The oxygen probe was calibrated by independent sampling and Winkler titration following Labasque et al. (2004) (and references therein). The calibration samples were spread over the whole campaign to cover different biogeochemical provinces. ¹⁴⁸ Dissolved oxygen from the Winkler titrations and from the CTD probe are well ¹⁴⁹ correlated ($R^2 = 0.98$) and the values measured by the CTD probe can be directly ¹⁵⁰ interpreted as oxygen concentrations (factor 1).

The Apparent Oxygen Utilization (AOU) was computed according to Garcia and Gordon (1992) as the difference between the saturation value (depending on the corresponding temperature and salinity) and the measured dissolved oxygen.

154 2.3. Biogeochemical and biological sampling.

155 2.3.1. Dissolved nutrients.

The seawater samples collected onboard for nutrient analysis were stored at -20° C for later analysis. The common nutrients concentrations - namely nitrate + nitrite, silicate and phosphate - were then determined in the labs (on land) by colorimetric methods using an Technicon Autoanalyser II, following the protocols and methods described in Aminot and Kerouel (2007).

161

162 2.3.2. Phytoplanktonic pigments.

The water samples for photoactive pigments analysis were collected at 2 or 3 depths and then were vacuum filtered through 25 mm diameter Whatman GF/F fiber glass filters (0.7 μ m particle retention size). Filtered volumes varied between 3 l in the offshore waters and less than 1l for some stations inside the coastal upwelling zone. The filters were immediately stored in liquid nitrogen until analysis on land. Among the total 219 samples, 16 were replicated and then analysed almost $_{169}$ simultaneously by two laboratories to perform a cross-validation ².

Phytoplankton pigments composition was determined by High Performance Liq-170 uid Chromatography (HPLC) methods. The filters were extracted and then rapidly 171 analysed (within 24 h) by HPLC with a complete Agilent Technologies system. Fol-172 lowing an adaptation of the method described by Heukelem and Thomas (2001), 173 the concentrations (in mg/m^3) of 13 separate phytoplankton pigments (see Tab. 174 1) were calculated from the absorption spectra with an internal standard correc-175 tion and external calibration. With a lower limit of detection for chlorophyll a of 176 0.0001 mg/m^3 and an injection precision of 0.4 %, the accuracy of this method has 177 been largely proven (Ras et al., 2008). Additional pigments as phaeophorbide a 178 (phaeo-a), chlorophyllide a (chloid-a) and divinyl chlorophyll a (div-chlo-a) were 179 measured only on a subset of the total samples. 180

While total chlorophyll *a* is the universal proxy for phytoplankton organisms, 181 accessory pigments are specific to phytoplankton groups (see Table 1), and their 182 respective proportion to total chlorophyll a is a proxy of the community composition. 183 Seven pigments are used as biomarkers of several phytoplankton taxa: fucoxanthin 184 (fuco), peridinin (peri), alloxanthin (allo), 19-butanoyloxyfucoxanthin (19-but), 19-185 hexanoyloxyfucoxanthin (19-hex), zeaxanthin (zea), total chlorophyll-b (chlo-b) (Ras 186 et al., 2008). These taxa are then gathered into three size classes (micro- M, nano-187 N, and picophytoplankton P), according to the average size of the cells (M cell size 188 $> 20 \ \mu m$, N size comprised between 2 and 20 μm , and P size $< 2 \ \mu m$). The fraction 189 of each pigment-based size class with respect to the total phytoplankton biomass is 190 calculated following Ras et al. (2008). 191

²On the common pigments that both labs measured, a very good agreement was found: e.g. R^2 of 0.91 for *chlo-a*, 0.96 for *fuco* and 0.94 for *19-hex*

¹⁹² 2.3.3. Zooplankton sampling.

Zooplankton samples were collected during day and night at one CTD station out 193 of two or three, with the highest possible frequency. A WP2 plankton net (mouth 194 surface of 0.25 m^2) mounted with 200 μ m mesh size was used, and towed vertically at 195 around 1 m/s over the water column from 5 m above the sea floor, or 70 m depth, up 196 to the surface. The proper volume of water filtered was calculated using the effective 197 depth of the tow as measured by a cable meter. The sample was then splitted into two 198 fractions using a motoda box (Motoda, 1959) and a fraction was directly preserved 199 in formaldehyde for later digitalisation, whereas the other half sample was fixed on 200 a pre-weighted filter (200 μ m) and conserved at -20° C in individual sterile cases. 201

Net collected zooplankton subsamples were digitized using the Zooscan imaging 202 system (Gorsky et al., 2010) which is a high resolution waterproof scanner. Out-203 put raw images were processed enabling fast and reliable enumeration and mea-204 surements of objects (www.zooscan.com). A Motoda splitter (Motoda, 1959) was 205 used for subsampling to obtain appropriate concentration of organisms. The digi-206 tization generates a raw image and a metadata form compiling various information 207 for each sample. The outputs of the image process are a set of vignettes and an 208 associated file compiling many parameters for each object including shape, length, 209 size,...etc... When all samples were scanned and processed, an automatic sorting pro-210 cedure was applied (for further details see (Gasparini, 2007; Gorsky et al., 2010)) to 211 classify each vignette into coarse faunistical groups. In this work, living objects are 212 separated from the non-living objects (marine snow, particulate organic matter, ag-213 gregates, bubbles...) to quantify exclusively zooplankton individuals. Their biomass 214 was computed following an estimation of the biovolume based on size measurements 215 from the Zooscan. For Copepods, major and minor axes of the best fitting ellipse 216

were used whereas equivalent spherical diameter (ESD) was used for other organisms (Gorsky et al., 2010). Finally, two classes of size were defined by a limit volume of 1 mm³ that represent the small (Ciliates / small Copepods) and large individuals (large Copepods, Chaetognaths, meroplankton...) found in the area. Although the common criteria to differentiate micro- and meso- zooplankton is the body length, this biovolume approach is in accord with their distinct ecological function (Gorsky et al., 2010).

224 3. Results and Discussion.

225 3.1. Meteorological conditions.

Wind data from QuikSCAT scatterometer and from on-board measurement reveal that upwelling favourable wind conditions prevailed roughly during two months, from the end of July to the end of September 2007 (Fig. 2).

More specifically, strong equatorward winds from July 20^{th} to August 13^{th} were 220 observed. These conditions led to a well developed upwelling of cold nutrient enriched 230 waters (SST $\sim 15^{\circ}$ C) that spread within a ~ 100 km width coastal band, with around 231 4-5 upwelling filaments extending up to ~ 200 km offshore (see Fig. 3a1). Then a two 232 days period of moderate-strong northward winds (15 m/s) occurs from August 13^{th} 233 to the 15^{th} , mid-day (Fig. 2). After this short wind inversion, upwelling favourable 234 wind conditions prevailed during the first leg of the cruise with intense equatorward 235 wind (10 to 25 m/s) blowing during two weeks, from August 15^{th} to August 30^{th} . 236 These successive wind events led to the intensification of the coastal upwelling with 237 temperature near the coast dropping to less than 14° C on the 23^{rd} of August (Fig. 238 3b1). At this date, the main front is located at about ~ 150 km offshore (i.e. a 239 westward displacement of ~ 50 km in ~ 15 days), interrupted regularly by 4 main 240

mesoscale filaments extending almost zonally up to 300 kmoffshore. From the 1st of September, the winds are mainly equatorward but of lower intensity than the previous weeks (≤ 13 m/s).

Based on our analysis of Fig. 3 and of every clear daily satellite imagery dur-244 ing July/August/September 2007, we have observed a transition from highly mixed 245 upwelling conditions (\sim August) to a relaxation period with increasing stratifica-246 tion (early September) when the main upwelling front returned closer to the coast 247 $(\sim \leq 100 \text{ km})$ while large filaments kept on developing offshore (not shown). Note 248 that section EW1 was performed between August 21^{st} and 22^{th} under intense south-249 ward winds (~ 15 m/s), whereas they were weak and decreasing (< 5 m/s on 250 the 24^{th} of August) when sampling section EW2 ($40^{\circ}N$). The filament was surveyed 251 when equatorward winds have drastically decreased $(6 - 8^{th}$ September), while they 252 were still imposing a slight offshore Ekman drift in the surface layer. The relatively 253 calm conditions were adequate for filaments development and tracking. 254

255 3.2. Shelf circulation: upwelling currents and mesoscale structures.

The velocity data analysed in this section are exclusively coming from the 300 kHz LADCP along sections EW1 and EW2 (Fig. 4) and within the filament (Fig. 5). Data from the two vessel mounted ADCP (150 and 38 kHz) were however used for cross validation to confirm the circulation patterns discussed below.

A typical upwelling circulation can be identified along every zonal section, although other mechanisms (internal waves or vortices) certainly superimpose their dynamical signature. The typical upwelling circulation is especially marked during leg 1 when the favourable winds were very strong (i.e. EW1 section, Fig. 4a). Along-shore velocities are mostly southward, intensified at the surface, ranging from -0.1 to -0.15 at the sub-surface to ~ -0.25 m/s or more at the surface (Fig. 4a2).

Although slightly less intense than previous observations, this seems to match the 266 upwelling jet (PCC described by Peliz et al. (2002)). The cross-shore velocities are 267 mostly westward (offshore) at the surface: ~ -0.05 m/s with with some higher peaks 268 locally. It is mostly eastward (onshore) below: ~ 0.05 m/s over the deepest part of 269 the shelf where the upwelling front is found, but reaching sometimes up to ~ 0.15 270 m/s within the water column. While the larger patterns are consistent with and 271 can be attributed to the upwelling mechanism, the local extrema are most probably 272 associated with turbulence or internal waves. 273

Close to the coast, the currents exhibit a more complex pattern, with an onshore 274 flow over most of the water column accompanied with southward (EW1 Fig. 4a2) 275 or northward currents (EW2 on Fig. 4b2 and filament Fig. 5a2). These features 276 occurring at the inner shelf (within 35 km from the coast) have a strong barotropic 277 signal with velocities of around 0.1 m/s). Another strong poleward flow was observed 278 during the filament survey, when the upwelling favourable winds have decreased: it 270 is located further offshore ($\sim 40 - 70$ km) and intensified at the surface (up to 0.25) 280 m/s). Poleward flow has been documented along all eastern boundary currents and 281 in the region by (Peliz et al., 2005; Torres and Barton, 2007) who studied the counter-282 current IPC. However, given the fact that the poleward current intensified near the 283 shelf break and that it is discontinued in space and time, the present observations 284 are rather associated with mesoscale structures such as vortices or filaments (Relvas 285 et al., 2007). 286

At the inner shelf, these along-shore alternating flows resulted in a convergence zone at the base of the filament $(9.5^{\circ}W / 40.3^{\circ}N)$ and are consistent with the presence of a dipole, with a cyclonic mesoscale eddy on the northern part (EW1) and an anticyclonic one further south (EW2), promoting the extension of the filament. Sanchez et al. also documented the contribution of strong opposing subsurface flows to the generation of filaments at their base. Away from the coast (40-70 km), the filamental structure is associated with a strong offshore current in the surface layer and an onshore current below (Fig. 5a1), consistent with the westward extension of the filament (Fig. 3a and Fig. 7a).

The North-South section across the tip of the filament (~ 150 km off the shelf) 296 is used to characterize the importance of accompanying mesoscale structures for its 297 development. A strong surface cyclonic eddy is detected just south of the structure 298 (Fig. 5b), characterized by eastward (0.15 m/s at 40.25°N) and westward velocities 290 $(< -0.25 \text{ m/s} \text{ at } 40.3^{\circ}\text{N})$. A subsurface anticyclonic vortex is observed north of the 300 filament: westward velocities of 0.1 m/s located at 40.43°N from the surface until 301 60 m associated with eastward velocities of -0.1 m/s at 40.45°N (30-60 m). This 302 dipole of coupled cyclonic and anticyclonic eddies located respectively south and 303 north of the filament advects coastal upwelled waters offshore (-0.1 to -0.25 m/s). 304 Even though other mechanisms could explain these velocity patterns, note that they 305 are consistent with the mushroom shape observed at the tip of the filament (Fig. 306 7a), typical of dipolar structures. Below the filament (45 to 60 m), at 40.375°N, a 307 counter jet (~ 0.1 m/s eastward) is observed and seems related to the subsurface 308 onshore flow, already observed along the EW section (Fig. 5a1), which accompanies 309 and compensates the offshore extension of the filament at the surface (García-Munoz 310 et al., 2005). 311

Overall, a strong (sub)mesoscale signal superimposes on the large scale classical upwelling flow, in particular due to the formation of eddies and filamental structures and their associated dynamical signatures. This smaller scale signal is indeed particularly clear for both EW2 and filament sections, when the wind had decreased and the main upwelling development was less intense. The offshore export of surface waters within the surveyed filament and its offshore extension are intensified due to

the dipolar structure at its tip, likely due to flow instabilities. Finer scale variability, 318 cause by internal wave activity (Quaresma et al., 2007) and submesoscale processes 319 (Capet et al., 2008), has been observed but not analyzed in detail. This pictures the 320 following scenario during wind relaxation phases: due to bottom friction, the main 321 upwelling circulation system rapidly decreases above the shelf in shallow water areas, 322 but remains active in regions with larger depths. Mesoscale features, developing at 323 the edge of the offshore upwelling front or directly above the shelf, then dominate the 324 shelf dynamics. Apart from flow instabilities, other mechanisms can be invoked to 325 explain the origin of the (sub)mesoscale signal: local wind variations (Relvas et al., 326 2007), the signature of local buoyancy forcing as the Western Iberian Buoyant Plume 327 (WIBP) (Peliz et al., 2002) or the interactions of the upwelling jet with bottom to-328 pography (Meunier et al., 2010). Our observations do not allow determining the 329 main process responsible for the extreme variability of the shelf circulation, and thus 330 further observational as well as modelling studies are needed. 331

332 3.3. Cross-shore physical variability.

333 3.3.1. Description of the successive upwelling fronts.

Along EW2 (at 40°N, Fig. 6b, c, d), a first feature can be identified with a clear 334 uplift of salinity, temperature and density surfaces within 10-20 km from the coast. 335 This coastal upwelling composed of waters reaching 14°C at the surface is likely to 336 result from the most recent pulse of equatorward winds. Considering a westward drift 337 of about 0.05-0.1 m/s (see section 3.2), this upwelling front might be "aged" of about 338 2-4 days. The shelf waters lying on the bottom (i.e. constituting the source waters) 339 are characterized by $\sigma_{\theta} \sim 26.45$, S ≥ 35.75 and T $\sim 13.2^{\circ}$ C. These characteristics 340 match the definition of the Eastern North Atlantic Central Water from Subtropical 341 origins (ENACWst), defined by (Varela et al., 2005) as waters with $T > 12.5^{\circ}C$ and 342

S \geq 35.7. Another specific upwelling front is located between 30-50 km, with again clear salinity, temperature and density fronts. It may correspond to a previous wind pulse that occurred 5-8 days ago. Other frontal features, such as the one identified between 65-75 km from the coast, could either correspond to even older upwelling events (10-15 days) or mesoscale features. The lighter and warmer surface waters ($\sigma_{\theta} < 26.2$) are pushed offshore (further than 80 km) by the Ekman drift associated with the equatorward winds.

Similarly, Rossi et al. (2010) analysed the upwelling dynamics based on section EW1 (at 41°N) and found that the coastal upwelling was also associated with cold ($\leq 13^{\circ}$ C) and dense waters ($\sigma_{\theta} \geq 27$) within 20 km from the coast. The previous upwelling fronts were located at ~ 30-55 km (also influenced by the secondary upwelling, see Rossi et al. (2010)) and at 65-85 km. The lighter surface waters ($\sigma_{\theta} \simeq 26$) were observed further offshore (> 90 km).

The relaxation of the equatorward winds (upwelling favourable) when sampling 356 EW2 as compared to EW1 (see Fig. 2) can be responsible for the small differences 357 observed between these two cross-shore sections. It is also evident that the alongshore 358 variability plays a key role in the IPUS. Indeed, based on a thorough analysis of a T-S 359 diagram using the entire dataset (including a North-South section not presented in 360 this manuscript), Rossi (2010) examined the origins of the upwelled waters along the 361 coast. It was found that the coastal upwelling sources its waters from two different 362 water masses depending on the latitude concerned. Along EW1 (at 41° N), the shelf 363 waters lying on the seabed were characterized by $\sigma_{\theta} \simeq 27.1$, S ≤ 35.7 and T = 12.3°C 364 (see also Rossi et al. (2010)). They thus matched the description of the Eastern North 365 Atlantic Central Water from Subpolar origins (ENACWsp) as defined by (Varela 366 et al., 2005); whereas the source waters along EW2 (about 100 km further south 367 than EW1) were identified as ENACWst. Note that instead of a sharp latitudinal 368

delimitation, there is probably a gradual transition from ENACWst to ENACWsp around $40 - 41^{\circ}$ N, so that a mixing between the two end-member of these subsurface water masses might indeed constitute the source of the upwelling in the northern IPUS.

Another feature of interest is the low salinity surface plume (≤ 35.7) observed 373 between 20 and 80 km from the coast at 41°N (EW1, Fig. 6a) whose origin is unclear. 374 Low salinity waters are also found just above the seabed, indicating a possible origin 375 from the deep slope waters (ENACWsp > 150 m) being upwelled onto the shelf. 376 Another possible explanation is the influence of the WIBP (S < 35.7) (Peliz et al., 377 2002) at the northern tip of the IPUS, related to the freshwater discharge from the 378 Galician Rias and Northern Portuguese rivers (the most significant discharges being 379 from the Minho and Douro rivers). However, because of the moderate freshwater 380 input during the upwelling season, the low salinity signal might indeed originate 381 from both the moderate rivers' input mixed with the recently upwelled ENACWsp. 382 Interestingly, the low salinity plume is observed at 40°N (EW2, Fig. 6b) between 383 45 and 80 km, further offshore than along EW1 (Fig. 6a). The thickness of this layer 384 of less saline water ($\sim 30\text{-}40 \text{ m}$) is maintained during its south-westward drift by the 385 PC/PCC. However its width had decreased from 60 (EW1) to 35 km (EW2). Otero 386 et al. (2008) studied the dynamics and extension of this low salinity lens, showing 387 that it is highly influenced by the wind regime and the shelf circulation (i.e. PCC and 388 IPC). The freshwater plume is confined at the coast when poleward winds prevail, 389 whereas it is exported offshore and southward under upwelling favourable wind, as it 390 is the case here. Some studies also emphasized the crucial role this physical feature 391 has on the biological activity, from plankton (Ribeiro et al., 2005) to fish recruitment 392 (Santos et al., 2007). 393

³⁹⁴ 3.3.2. Structure of the mesoscale filament.

The dimensions of the filament surveyed early September are ~ 160 kmin length 395 $(\sim 2^{\circ})$ for a coastal base of almost ~ 100 km (1°), getting slimmer offshore ~ 25 396 km (see Fig.7a). The tip of the filament has a mushroom shape, associated with 397 opposite sign submesoscale vortices on each side (see sect. 3.2). The coastal waters, 398 characterized by relatively colder temperature (~ $16 - 18^{\circ}$ C) than surrounding 399 $(\sim 18 - 19^{\circ}C)$ are advected till 160 km offshore. No successive fronts are observed 400 in the filament as compared to EW transects (see sect. 3.3.1). The surface layer 401 constituting the filament is composed of slightly lighter waters (cold and fresh), 402 providing a buoyant input to the structure. In addition, the thermocline is relatively 403 shallow inside the filament and its base reveals vertical displacements of more than 404 20 m which may be linked with submesoscale vortices or internal waves (Relvas et al., 405 2007). The present snapshot does not allow distinguishing between these processes. 406 The transition between the filament waters and the open ocean is observed at around 407 160 km with a deepening of the Mixed Layer Depth (MLD). 408

On the North-South section carried out about 145 km offshore, the filament is 409 clearly identified from 40.3° to 40.45°N by local extremes in temperature and salinity 410 both at the surface and the subsurface (Fig. 8a, b). A temperature minimum is 411 observed at the surface (~ 2° colder than the surroundings), accompanied by a 412 uplift of the thermocline at the subsurface (from 50 m outside to 35 m within the 413 filament). The core of the filament is characterized by a surface minimum of salinity 414 (~ 35.75 down to 50 m, i.e. ~ 0.1 psu lower than the surroundings) that lies above 415 a sub-surface salinity maximum (> 35.9 from 50 to 100 m). 416

The low salinity tongue (< 35.7), possibly originating from the coast, is also observed within the filament (Fig. 7b). Likely to be composed of the WIBP mixed with the ENACWst/sp recently upwelled, these "fresh" waters have been advected inside the filament up to 140 km offshore (against 80 km for the EW section). Consistently, the meridional section across the tip of the structure (Fig.8b) revealed a salinity minimum. All our observations agree with Peliz et al. (2002) and suggest that the characteristics of the filament (buoyant waters in its core and the presence of mesoscale eddies at its tips) favour a preferential conduct for exchanges between coastal and offshore waters.

426 3.4. Contrasting biological responses.

427 3.4.1. Chlorophyll a distribution from the fluorometer.

The general satellite-derived chlorophyll *a* pattern shows maximal concentrations of $1 - 10 \text{ mg/m}^3$ at the coast, while the offshore waters are relatively poor ~ 0.1 mg/m³ or less (Fig. 3a2, b2). These two sub-domains are sharply delimited by the upwelling front at ~ 150 km off the coast, while mesoscale filaments with moderate surface chlorophyll *a* concentration (0.1 - 1 mg/m³) extend up to ~ 200-300 km offshore.

The successive upwelling fronts examined previously along both EW transects 434 (section 3.3.1) are marked with a local surface maxima in chlorophyll a, almost 435 equally distributed from the surface down to 30-40 m(Fig. 9a, b). These fronts 436 gradually advected offshore have been analysed by Rossi et al. (2010) along EW1 437 and are also observed along EW2 (Fig. 9b). The most recent upwelling event is 438 characterized by high chlorophyll a concentrations $(1-3 \text{ mg/m}^3)$ within 20 km from 439 the coast, then comes the previous one between 30 and 50 km supporting the highest 440 chlorophyll concentrations $(1-10 \text{ mg/m}^3)$. The maximum response of the ecosystem 441 in terms of chlorophyll a is found over the mid-shelf, developing shortly (about 5-8) 442 days) after the initial upwelling pulse. Finally the most ancient front is found offshore 443

between 65 and 75 km with moderate chlorophyll *a* content $(0.3 - 1 \text{ mg/m}^3)$ some 10 to 15 days after the pulse. The ancient front along EW1 also concerns similar chlorophyll *a* concentrations $(0.5 - 1 \text{ mg/m}^3)$ and extends until 85 km against 75 km for EW2, which correspond to a westward drift of about 10 km during 3 days. Note that the coastal areas (< 20 km) along EW1 are quite poor in chlorophyll *a* probably due to the fact that the sampling was carried out exactly during the upwelling pulse.

Between each surface local maxima driven by upwelling pulses, moderate con-451 centrations are observed $(0.3 - 1 \text{ mg/m}^3)$, associated with a Subsurface Chlorophyll 452 Maximum (SCM) at ~ 25 m. The ecosystem responds specifically to intense tran-453 sient upwelling pulses with homogeneous and high chlorophyll a concentrations in 454 the mixed layer. In between these upwelling events, the biological activity is moder-455 ate and concentrated at the subsurface. These changes in the chlorophyll a vertical 456 distribution patterns are reflected in the planktonic communities adapted to each 457 particular environmental window (see also sect. 3.5). 458

Waters westward of the most ancient front (> 80 km) are characterized by a deeper SCM (~ 50-70 m) of lower chlorophyll *a* concentrations (< 0.5 mg/m^3) and poor surface waters (< 0.1 mg/m^3).

Overall, chlorophyll a concentrations inside the filament are relatively high (0.3 -462 3 mg/m^3) as compared to surrounding (0.01 mg/m³, Fig.7a2). Shelf concentrations 463 are around $1 - 10 \text{ mg/m}^3$ chlorophyll *a* within the filament (Fig. 9c), which is 464 similar to the level observed along EW2 but slightly more than along EW1 (1 -465 3 mg/m^3). EW2 and the filament were sampled some days after EW1 while the 466 winds weakened. Restratification after an intense upwelling pulse might allow larger 467 phytoplankton cells to grow and to use more efficiently nutrients brought previously 468 to the euphotic layer. In addition, elevated chlorophyll a concentrations are observed 469

within the filament until 160 km offshore, extending considerably (more than 100 km) the surface of biologically productive waters as compared to EW1 and EW2 (85 and 75 km respectively). Even across the tip of the structure (Fig. 8c), chlorophyll *a* concentrations are higher within the filament $(0.3 - 1 \text{ mg/m}^3)$ than outside $(0.1 - 0.3 \text{ mg/m}^3)$.

Another difference between the filament and the EW sections is the vertical repar-475 tition of chlorophyll a. Over the inner shelf (< 30 km) the phytoplankton is almost 476 equally distributed within the mixed layer (from the surface down to 40 m), whereas 477 a SCM appears at around 40 km, a smaller offshore distance than along EW sections 478 (Fig. 9). The SCM in the filament is situated between 20 to 50 m, following the 479 depth of the thermocline (as indicated by the isotherm 16 °C on Fig. 9c), varying 480 because of internal waves. It concerns moderate chlorophyll a concentrations (0.3-1)481 $\rm mg/m^3$) and it is shallower than the deep SCM (~ 50-70 m) characterized by lower 482 chlorophyll a levels (0.5 mg/m^3) found offshore both EW sections (> 80 km). At 483 about 150 km off the coast, the SCM still follows the thermocline situated at around 484 35 m in the filament, matching a maximum of Coloured Dissolved Organic Matter 485 (CDOM), whereas it is at 50 m outside (Fig.8c). 486

⁴⁸⁷ Note that within the filament, the successive upwelling pulses are not marked ⁴⁸⁸ in chlorophyll *a* as along EW sections, suggesting a relative homogenization of the ⁴⁸⁹ waters inside the filament.

490 3.4.2. Dissolved Oxygen.

It is worth noting that the minimum of dissolved oxygen (< 200 μ mol/kg), corresponding to a maximum of AOU (> 60 μ mol/kg) is found on the shelf bottom, while its lateral position coincides very well with the highest surface concentrations of chlorophyll *a* (see black isolines on Fig. 9a, b, c). It is a sign of an intense *in*- situ consumption of oxygen by the microbial remineralisation of the sinking organic
matter.

Although the horizontal extension of the local minimum of oxygen is quite similar 497 $(\sim 50 \text{ km})$ along both EW sections, its vertical thickness is higher at 40°N (up to 498 70 m) than at 41° N (less than 50 m), consistent with the chlorophyll *a* distribution. 499 As such, it seems that the intensity of the surface biological activity, related to the 500 amount of sinking organic matter in the water column, is the primary factor driving 501 the local remineralisation processes. However, other important factors are known 502 to influence microbial remineralisation, such as the terrestrial inputs, the alongshore 503 circulation, itself influenced by the width of the shelf (residence time), the benthic 504 processes (Alvarez-Salgado et al., 1997). Note that the near bottom areas with 505 maximum AOU concentrations (up to > 100 μ mol/kg) are also marked by elevated 506 turbidity (not shown). It suggests that resuspension processes from the sediment 507 by tidal currents and internal waves might play a key role in these remineralisation 508 patterns (Alvarez-Salgado et al., 1997; Quaresma et al., 2007). 509

The local minimum of oxygen below the filament presents the maximal spatial 510 extension (till ~ 150 m deep and 60 km from the coast) and reaches the lowest levels 511 of dissolved oxygen recorded, such as 115 μ mol/kg (AOU up to > 110 μ mol/kg). 512 Further offshore (Fig.8c, d), the SCM at ~ 30 m matches with a minimum of AOU 513 $(-15 \ \mu mol/kg \ symbolizing \ a \ strong \ oxygen \ production \ by \ photosynthesis)$. The 514 signature in AOU is detectable at the subsurface with a local maximum (>35 515 μ mol/kg) doming right under the structure (130-200 m). Although lateral advection 516 might affect the vertical export of organic matter, this observation suggests that the 517 product of the relatively high surface biological production within the core of the 518 filament is also exported deeper in the water column and remineralized. It highlights 519 the importance of such structure for new as well as regenerated production. 520

⁵²¹ 3.4.3. Dissolved Nutrients.

Nutrient concentrations in the mixed layer (down to 40 m) within the most re-522 cently upwelled waters (less than 30 km from the coastline) range around 10 - 12523 μ mol/l for nitrate (Fig.10a), ~ 1 μ mol/l for phosphate and ~ 6 μ mol/l for silicate 524 (not shown). Cravo et al. (2010) compiled several nutrients values from the litera-525 ture and our values are found in the upper range of their dataset, attesting of the 526 strong upwelling event sampled. Then, in the former upwelling front (30-50 km), 527 they decrease down to $2-5~\mu$ mol/l, $0-0.4~\mu$ mol/l and $1-2~\mu$ mol/l for nitrate, 528 phosphate and silicate respectively. Finally, more than 65 km from the coast, the ni-529 trate concentration are below detection levels, whereas low concentrations of silicate 530 $(0.3 - 0.7 \,\mu \text{mol/l})$ and phosphate $(0.1 \,\mu \text{mol/l})$ remain (not shown). This gradual nu-531 trient depletion, similarly observed along EW1 (not shown) and within the filament 532 (Fig.10b), is likely to be due to constant phytoplankton uptake along the westward 533 drift of the freshly upwelled waters. The absence of nitrate offshore while silicate and 534 phosphate are still detectable reinforces the fact that nitrate is the limiting factor 535 for primary production in surface waters (Castro et al., 2000; Joint et al., 2001). 536 Another hypothesis that could explain this excess of silicate and phosphate is their 537 preferential remineralisation rate revealed by Alvarez-Salgado et al. (1997). 538

⁵³⁹ Note that a significant difference between EW2 and the filament remains in the ⁵⁴⁰ sub-surface waters (50-100 m). Moderate nitrate concentrations of $4 - 7 \mu \text{mol/l}$ are ⁵⁴¹ still observed just below the filament until 120 km offshore (Fig.10b), whereas it ⁵⁴² is less than 3 μ mol/l from 70 km off the coast along EW2 (Fig.10a). It could be ⁵⁴³ related to the maximum of AOU, sign of intense remineralisation processes, that was ⁵⁴⁴ observed just below the filament in sect. 3.4.2. In addition, the specific circulation ⁵⁴⁵ underneath the filament's core (Fig. 5a, b) might promote accumulation and *in-situ*

remineralisation of organic matter originating from the surface biological production. 546 Overall, the mean nutrient concentrations off the shelf break below 150 m (source 547 waters of the upwelling) are about 2/3 of what was measured at the inner shelf 548 bottom, as observed for the three macro-nutrients along transects EW1, EW2 and 549 the filament (Fig.10). It suggests that remineralisation processes account for about 550 1/3 of the nutrient available for the surface coastal ecosystem. This estimation is 551 in line with Alvarez-Salgado et al. (1997) who showed that nutrient remineralisation 552 tends to increase surface primary production by up to 50 %. 553

⁵⁵⁴ 3.5. Comparative analysis of the planktonic communities.

555 3.5.1. Phytoplankton communities.

The successive upwelling fronts along EW2 are characterized by high phytoplank-556 ton biomasses, as shown by 3 peaks of total chlorophyll a (from HPLC) at 15, 41 557 and 65 km (Fig. 11a). Shelf communities (< 50 km, associated with the two most 558 recent upwelling fronts) are largely dominated by micro-phytoplankton ($\sim 90 \%$) 550 in both surface and sub-surface layers (Fig. 11b, c). Cermeno et al. (2006) also 560 observed that microphytoplankton dominates the assemblage during an upwelling 561 event, while nano- and picophytoplankton are present in lower proportions. Surpris-562 ingly, both surface and subsurface communities composition changed clearly at the 563 transition between the 2 former upwelling fronts (i.e. at 55 km). In contrast with 564 the coastal upwelling communities, they are roughly composed of 50 % of micro-, 25 565 % of nano- and 25 % of pico-phytoplankton. Then, the size repartition of plankton 566 within the most ancient front at 65 km is indeed very similar to the coastal fronts. 567 Although it has a lower chlorophyll a content, probably due to the gradual nutrient 568 depletion during 8 to 10 days after the initial pulse, it is still dominated by micro-569 phytoplankton at the surface and the subsurface. Note that the low salinity plume 570

(grey contours on Fig. 9b) is constituting the most ancient front but not the coastal one, so that this feature can not solely explained the similar size structure of the phytoplankton. Both open ocean communities (> 80 km) are clearly different and are dominated by small size cells, with a composition of 45 % of pico-, 35 % of nanoand 20 % of micro-phytoplankton at the surface and the subsurface. Note that there is still a small proportion of microphytoplankton, suggesting that passive advection of chlorophyll-*a* through the front occurs (see also sect. 3.4.1 and 3.6).

Within the filament, the relative proportion of micro-phytoplankton over the 578 shelf (at 26 and 41 km) is around 80 %, similarly to EW sections (Fig. 12b, c). 579 From 60 km off the coast (63, 107 and 151 km), it reduces to 30 % or less , while 580 being replaced by nanoplankton which reaches ~ 50 % in the surface waters and even 581 more in the SCM. Pico-plankton represents about 25 % of the population everywhere. 582 Such an high proportion of nano-plankton population is not being observed along the 583 EW sections or offshore. It shows that middle size classes of phytoplankton (nano-, 584 including mixotrophs) are favoured within the filament, whereas at a similar offshore 585 distance in open ocean waters, the communities are pico-plankton dominated. Note 586 that the time lag of about 10-15 days between the sampling of the EW sections 587 and the filament added to the decrease of the upwelling favourable winds (see sect. 588 3.1) may also partly explain the dominance of nanophytoplankton in the filament. 589 However, because of the similarities of the coastal and open ocean sites between these 590 two periods, it might only affect slightly our interpretations. Another noticeable 591 difference between the communities outside the filament (195 km) and those inside 592 (151 km) is the proportion of micro-phytoplankton. They are still more abundant 593 in the filament (50 and 25% at the surface and subsurface respectively) than in the 594 open ocean (25 and 10%), being brought from the coastal areas within the filament. 595 The pigments concentration from HPLC can also provide broad information about 596

the phytoplankton assemblages across the successive fronts. Considering the acces-597 sory pigments known to be specific of certain micro-phytoplankton, we observed that 598 the shelf areas are characterized by high concentrations of *fuco* and *peri* indicating 590 that diatoms and dinoflagellates dominate the micro-phytoplankton population (Fig. 600 11a, b). Note that the maximum of *fuco* and *peri* is found slightly offshore the coastal 601 front. These populations of large cells are known to have a relatively slow develop-602 ment (Tilstone et al., 2003; Ras et al., 2008) and thus seem to appear after a slight 603 time lag ($\sim 2-4$ days) as compared to the immediate coastal upwelling. 604

Conversely, Chlo-b concentrations are high close to the coast suggesting an im-605 mediate response of green algae. Crytophytes, cyanobacteria and prochlorophytes 606 (xea) are also present in the most recent upwelling front, within 15 km from the 607 coast. The distribution of volatile halogenated organic compounds was simultane-608 ously investigated in the IPUS by Raimund et al. (2011) and a coastal source was 609 evidenced, possibly related to these near-coastal communities. When moving away 610 from the coast, *peri* increases when *fuco* decreases (55 and 64 km), suggesting that 611 dinoflagellates predominate over diatoms when nutrient concentrations diminish dur-612 ing the westward drift in the ancient front. This population shift between diatoms 613 and dinoflagellates, of slower development, has been described by Joint et al. (2001) 614 in a lagrangian water mass experiment. Resende et al. (2007) also observed the oc-615 currence of diatoms close to the coast, whereas dinoflagellates are found offshore after 616 the upwelling relaxation when silicate are depleted. These mixotrophs are able to 617 use directly the particulate organic matter, taking advantage on the ageing diatoms. 618 Cyanobacteria and prochlorophytes (*xea*) are present everywhere along section EW2 619 but highest concentrations occur at 55 km, i.e. between the upwelling fronts where 620 a SCM is observed. At the same location (55 km) and at 64 km offshore, elevated 621 concentrations of 19-hex represent a population of haptophytes, indicating the pres-622

ence of specific communities between the upwelling fronts and at the transition with the oligotrophic waters. Further than 80 km from the coast (85 and 92 km), the open ocean communities are composed of nano- (haptophytes, *19-hex*; green algae, *chlo-b*) and pico-plankton (cyanobacteria and prochlorophytes, *zea*). This is in very good agreement with the analysis of Tilstone et al. (2003); Lorenzo et al. (2005) who described the shelf phytoplankton communities as diatoms and dinoflagellates dominated, whereas cyanobacteria are found in the oceanic waters.

Similar conclusions about the phytoplankton assemblages can be drawn from the 630 planktonic community of the filament (Fig. 12a), although some differences remain. 631 In particular, the total chlorophyll a (HPLC) is still significant 150 km offshore with 632 0.8 mg/m^3 , whereas it was below 0.1 mg/m^3 from 70 km along the EW sections, 633 strengthening the results from sect. 3.4.1. Although diatoms and dinoflagellates 634 are present above the shelf, the dinoflagellate population seems larger than along 635 EW2 (up to 0.15 mg/m^3 of *peri* in the filament against $0.05-0.1 \text{ mg/m}^3$ along EW2). 636 When moving offshore, these large cells are replaced by smaller ones: cyanobacte-637 ria, prochlorophytes (zea, div-chlo-a) and prymnesiophytes (19-hex) increase rapidly 638 (Fig. 12a). Another significant difference is the concentration of 19-hex: it is 0.25 639 mg/m^3 until 150 km offshore within the filament but $\leq 0.1 mg/m^3$ along EW2 from 640 70 km). These pico- and nano-phytoplankton dominate the communities within 641 the filament, in line with Barbosa et al. (2001) who found that bacterioplankton is 642 around 15 % of the total plankton community production over the shelf, whereas it 643 can reach about 40 % under more oligotrophic conditions in a filament. 644

Although our analysis focusses on the cross-shore evolution of the phytoplanktonic communities, it is clear that the alongshore advection of the local water masses (see sect. 3.2 and 3.3.1) introduces additional variability not analysed here.

648 3.5.2. Zooplanktonic biomasses.

The highest zooplankton biomass is found at the coast and decreases when moving offshore (Fig. 11d and Fig. 12d, black lines). In near coastal areas (< 30 km), zooplankton is dominated by small individuals among whom copepods represent 70 to 80 % of community biomass (not shown). Small sized copepods are important phytoplankton grazers (Landry and Calbet, 2004) and their intense grazing pressure is likely to participate in the observed reduced phytoplankton biomass near the coast (see sect. 3.4.1 and 3.5.1), as already suggested by Fileman and Burkill (2001).

Large individuals dominate from 30 to 50 km (Fig. 11d and Fig. 12d) and con-656 stitute a "transitional" community. Zooplankton groups such as Oithona Copepods, 657 Chaetognaths, Bryozoan larvaes, Bivalves and Appendicularians prevail there. The 658 presence of Bryozoan larvaes (meroplankton released by neritic benthic adults) at 659 the mid- and outer-shelf suggests that this zooplankton community originated from 660 the coastal upwelling and have then been gradually exported offshore, in line with 661 our previous analysis (sect. 3.3 and 3.5.1). The presence of Chaetognaths, preda-662 tors of Copepods (Duró and Saiz, 2000), indicates the establishment of a mature 663 zooplankton community with secondary consumers trophic levels. Within 15-60664 km from the coast, the micro-phytoplankton, especially diatoms (Fig. 11a, red line), 665 responds quickly (2-4 days) to the successive upwelling pulses and dominates the 666 shelf assemblages. These high levels of microphytoplankton biomass may contribute 667 to sustain the longer development of the large zooplankton organisms during their 668 offshore drift, explaining why they dominate only from ~ 30 km (i.e. about 5-10 669 days after the initial pulse). This is in good agreement with Queiroga et al. (2005) 670 who also documented the apparition of both meroplankton and planktonic preda-671 tors during the offshore displacement of a coastal zooplanktonic community in the 672

673 upwelling season.

Note that large zooplankton organisms are still observed as far as 150 km offshore 674 within the filament (~ 100 mm³/m³ BV, Fig. 12d), whereas they were completely 675 absent from 70 km along EW2 (Fig. 11d). the frontal structure (EW1, EW2) seems 676 to strongly isolate large zooplankton individuals from the open ocean (Landry et al. 677 (2012) and references therein), so that the location of the upwelling front (itself 678 driven by the successive pulses of equatorward winds) may set the maximal offshore 679 extension of these large organisms which are an important food source for exploited 680 higher trophic levels. Unfortunately, the lack of sampling at high spatial resolution 681 near the physical boundary does not allow us to conclude firmly. It also shows that 682 the "transitional" community drift further offshore and thus develop a longer time 683 within the filament than along the EW1/EW2 transect, where it is confined between 684 the mid-shelf and the most offshore upwelling front (~ 70 km). 685

Additional HPLC pigments such as phaeo-a (senescent diatoms) and chloid-a 686 (grazer fecal pellets) were exceptionally measured on a subset of the filament samples. 687 Both pigments are found in elevated concentrations until 60 km (Fig. 12a) indicating 688 that large zooplankton grazers feed on micro-phytoplankton. Their concentrations 689 decrease when moving offshore but level of *chloid-a* remains slightly higher within 690 the filament ($\geq 0.1 \text{ mg/m}^3$) than in the open ocean ($\sim 0.06 \text{ mg/m}^3$ at 195 km). It 691 indicates a more intense zooplankton grazing within the filament than in the open 692 ocean, proof of a dynamical ecosystem exported offshore within the structure. 693

The offshore oligotrophic ecosystem is characterized by low biomass of small organisms (> 70 km for EW2 on Fig. 11d and > 160 km for the filament on Fig. 12d), essentially composed of \sim 50 % of small Copepods and \sim 50 % of Cladocera (not shown). In the open ocean (offshore the main front and outside the long filaments), the size-structure of the oligotrophic ecosystem seems in equilibrium ⁶⁹⁹ with both phyto- and zooplankton communities dominated by small organisms.

700 3.6. Estimation of offshore transport and chlorophyll fluxes.

In this section, we calculate estimates of offshore transport and chlorophyll fluxes through the filament and across the upwelling front based on a typical situation of the north-western Iberian margin during upwelling season (see Fig. 3b1). The upwelling front extends meridionally from $\sim 37^{\circ}$ N to $\sim 43.5^{\circ}$ N (720 km) and is interrupted by four large filaments. In approximation, the system can thus be separated into 4 filaments, each having about 70 km width, and a more regular quasi-meridional semi-continuous front extending over 440 km.

The currents derived from the LADCP at 10.6°W (see Fig. 5b) allow us to 708 evaluate the offshore transport induced by the filament at its tip. Using the horizontal 709 boundaries from 40.3° to 40.45°N with a vertical extension of 50 m, a westward 710 transport of ~ 0.16 Sv due to the filament is estimated. This falls within the lower 711 range of the compilation of observations of upwelling filaments by Sanchez et al., 712 probably because the transport is computed at the tip of the filament. By multiplying 713 the westward velocities by the chlorophyll content (averaging to 0.55 mg/m^3), a flux 714 of chlorophyll of around 0.016 mg m⁻² s⁻¹ is obtained. Integrating this value over 715 its cross-section (50 m for 0.15° of latitude) yields to about 82.5 g/s of chlorophyll 716 a transported offshore at the tip of the filament, in very good agreement with the 717 flux of 70.7 g/s calculated by García-Munoz et al. (2005) in the Canary upwelling 718 system. 719

To approximate the cross-shore transport of near-coastal water masses due to this structure, we consider the westward velocities recorded at the tip of the filament as similar to the ones during its initiation ($\sim 0.11 \text{ m/s}$). In addition, we integrate Chlorophyll *a* concentrations from the coastal areas ($\sim 1 \text{ mg/m}^3$) over the dimensions

deduced previously (70 km width for a thickness of 50 m). It is found that about 0.4 724 kg s⁻¹ of chlorophyll a can be exported off the shelf by this single filament. Although 725 all variables (dimensions, velocities and chlorophyll a concentration) are time and 726 space dependent, this number is consistent with other estimates of offshore transport 727 of biogeochemical properties as given by Alvarez-Salgado et al. (2001); García-Munoz 728 et al. (2005); Alvarez-Salgado et al. (2007); Cravo et al. (2010). The seaward flux 729 of chlorophyll through the surveyed filament can be multiply by 4 to estimate the 730 "filament contribution" to cross-shore transport under a typical upwelling favourable 731 season. It is of the order of 2 kg s⁻¹ of chlorophyll a exported from the shelf toward 732 the open ocean by filamental structures over the north-western Iberian margin. 733

Similar seaward transport estimates can be done through the regular upwelling front. The westward velocities are of the order of 0.05 m/s on average over the Ekman layer of about 50 m thick. By multiplying the westward velocities with the chlorophyll content over the shelf ($\sim 1 \text{ mg/m}^3$) and integrating this value over the front (50 m deep for a length of 440 km), it is found that a flux of more than 1 kg/s of chlorophyll *a* is occurring from the shelf toward the open ocean through the front between 37°N to 43.5°N.

Although these calculation contains numerous biases and approximations, it gives 741 an estimate of the cross-shelf exchanges mediated by both structures within the 742 Iberian Upwelling System. Covering only $\sim 40 \%$ of the total length of the upwelling 743 front, the filaments are responsible of more than 60 % of the cross-shelf transport, due 744 to the intense offshore advection of coastal ecosystem. In addition, these filamental 745 structures can transport coastal water masses further offshore (> 200 km) than 746 through the upwelling front. We hypothesised that under intense upwelling pulses, 747 the front has a large impact on the cross-shore transport, whereas the effect of self-748 propelled filaments become dominant under relaxation period. 749

750 4. Conclusions.

During the MOUTON multidisciplinary survey in August/September 2007, strong equatorward winds promoted upwelling development with temperature dropping below 13°C at the coast and chlorophyll *a* concentrations increasing up to 10 mg/m³. The cross-shore gradient was examined by comparing two East-West transects through the upwelling front and one survey of a mesoscale filament.

Our analysis emphasized the role of mesoscale features such as eddies and filaments that superimpose their dynamical signature on the classical upwelling flow. Nevertheless, surface velocities often directed to the west produce a significant offshore transport through the meridional upwelling front. This transport is intensified within the filament surveyed due to the presence of mesoscale dipolar eddies at the base and tip of the elongating structure.

The EW sections are marked by sharp temperature fronts due to the successive upwelling pulses that bring cold/fresh/enriched waters (ENACWsp and ENACWst) to the coast. These consecutive fronts, characterized by elevated chlorophyll *a* concentrations in the mixed layer, are gradually advected (south)westward by the upwelling currents. During relaxation phases (between fronts), the biological activity is concentrated at the subsurface and still concerns higher levels than in the oligotrophic waters observed from 80 km off the coast.

Composed of the recently upwelled ENACW mixed with the WIBP, low salinity waters provide a buoyancy input to the filamental structure promoting its offshore elongation. In contrast with EW sections, the water is relatively homogeneous within the 3 dimensional filamental structure but well isolated from the surrounding. The resulting biological response is organised as a shallower subsurface maximum extending far offshore (up to 160 km). High surface chlorophyll *a* concentrations are associated with low oxygen levels at the subsurface, a sign of nutrient remineralisa-tion processes that are favoured below the filament.

The variability of water mass properties, including their stratification, nutrient 777 contents and maturation state, is impacting strongly the planktonic communities. 778 Coastal areas (< 20 km) support a quick response of small phytoplankton, followed 779 2-4 days later by micro-phytoplankton which dominate largely the coastal upwelling. 780 The zooplankton population at the coast is mainly composed of numerous small 781 copepods imposing a high grazing pressure and associated with a strong export of 782 organic matter. Slightly offshore (between 30 to 60 km, i.e. 5-10 days), dinoflagel-783 lates gradually overshadow diatoms while large individuals of zooplankton dominate. 784 Being relatively isolated for a longer offshore drift, the coastal ecosystems embed-785 ded inside the filament evolve differently. Coastal waters are also dominated by 786 micro-phytoplankton but higher proportions of nano-plankton are observed in the 787 filament (> 60 km) due to the nutrient depletion promoting mixotrophy. Strongly 788 contrasting with the coastal and transitional areas, oligotrophic assemblages found 789 offshore are characterized by small-size individuals and low biomasses for both zoo-790 and phytoplankton. 791

Comparing the hypothetical cross-shore transport mediated by the two structures, 792 it is shown that filaments, although less extended meridionally than the upwelling 793 front, are responsible of a greater offshore flux of chlorophyll. Due to their specific 794 physical structures, filaments act as preferential conducts for seaward transport of 795 productive coastal waters. We speculate that upwelling fronts, regularly pushed off-796 shore by transient favourable winds, have a large importance in cross-shelf exchange 797 at short time scales, whereas the effect of filaments dominates under relaxation pe-798 riod, maintaining a constant fuelling of the oligotrophic open ocean. 799

To further estimate the role of prominent filamental structures on the metabolic

⁸⁰¹ balance of the North-Atlantic gyre, extensive observations must be carried out. Con-⁸⁰² stant monitoring through an integrated marine observing system (including moored ⁸⁰³ buoys, regular glider deployments, high frequency radars and ship-based survey) ⁸⁰⁴ could be implemented at specific locations in the IPUS where the formation of such ⁸⁰⁵ filaments is favoured (e.g. capes, promontory). Another important project is to ⁸⁰⁶ pursue the development of 3D coupled models at high resolution of the IPUS, whose ⁸⁰⁷ validation could obviously benefit from the present results.

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HPLC measured pigments	Abbreviations	Size classes	Taxonomic or biogeochemical significance
Chlorophyll a	chlo-a	All	All - except Prochlorophytes
Chlorophyll b	chlo- b	P + N	Green algae
			(Chlorophytes, Prasinophytes)
Peridinin	peri	М	Dinoflagellates
Fuc ox anth in	fuco	М	Diatoms , Prymnesiophytes,
			and some Dinoflagellates
Z eax anth in	zea	Р	Cyanobacteria, Prochlorophytes
Alloxanthin	allo	P + N	${f Cryptophytes}$
19-But an oyloxy fuc ox anth in	19-but	Ν	Prymnesiophytes, Pelagophytes
19-Hexanoyloxy fuc oxanthin	19-hex	Ν	Prymnesiophytes (Haptophytes)
Divinyl Chlorophyll a	div- $chlo$ - a	Р	Prochlorophytes
Chlorophyllide a	chloid- a	-	Senescent diatoms
Phaeophorbide a	phaeo-a	-	Grazor fecal pellets

Table 1: List of the pigments used in this study and their taxonomic significance. A few characteristic pigments (bold letters) were associated to particular algal groups to describe the phytoplankton community, following Ras et al. (2008). The last four pigments were additionally measured on a small subset of the total samples.



Figure 1: Overview of the MOUTON 2007 oceanographic campaign in the Iberian Peninsula Upwelling System. Colored diamonds represent the CTD stations organised as transects (red for East-West sections: EW1 at 41° and EW2 at 40°; blue for the filament network). Black contours represent the bathymetry (in m). A map of south-western Europe and north Africa is displayed on the upper left insert, with a red rectangle highlighting the surveyed area.



Figure 2: Wind (in m/s) vectors from the QuikSCAT scatterometer (averaged over the surveyed area $39 - 43^{\circ}N / 9 - 12^{\circ}W$) and the onboard measurements (during both legs of the survey, as shown by the black segments). Black dotted segments indicate when the transects of interest were carried out. The wind vectors emanate from equally spaced points along the horizontal x-axis, while the vector components are expressed relative to the origin of the respective vector. The vectors pointing down (up, respectively) represent a wind blowing southward (northward, respectively) of intensity directly readable on the y-axis.



Figure 3: Daily Sea Surface Temperature (°C) and Chlorophyll- $a \text{ (mg/m^3)}$ from MODIS Aqua for a) 7th August 2007 and b) 23rd August 2007. White areas are clouds and black contours represent the bathymetry (200, 500, 1000 and 2000 m). On lower panels b1) and b2), the white segments represent the cross-shore sections EW1 and EW2.



Figure 4: Cross-shore (a1, b1) and along-shore (a2, b2) velocities (m/s) derived from the LADCP along EW1 at 41°N (a) and EW2 at 40°N (b). On the upper panels blue color indicates west-ward/offshore current and red color eastward/onshore. On the lower panels, red color represent northward current and blue color southward. The white thin lines indicate the measurement positions; the thick black lines represent the observed bathymetry. The black annotations represent an illustrative sense of the circulation.



Figure 5: Cross-shore (a1, b1) and along-shore (a2, b2) velocities (m/s) derived from the LADCP along the East-West transect within the filament (a) and the North-South section across its tip at 10.6°W (b). On the upper panels blue color indicates westward/offshore current and red color eastward/onshore. On the lower panels, red color represent northward current and blue color southward. The white thin lines indicate the measurement positions; the thick black lines represent the observed bathymetry; the black rectangles identify the core of the filament. The black annotations represent an illustrative sense of the circulation.



Figure 6: Distance from the coast (km) versus depth profiles of CTD sensors along both cross-shore transects. a) EW1 salinity; b) EW2 salinity, c) temperature (°C) and d) density (σ_{θ}). The black lines in the salinity sections contour the low salinity plume (< 35.7). The white vertical lines in d) indicate the measurement positions; the thick black line represents the observed bathymetry. Black dotted rectangles on panel c and d identify the successive upwelling fronts.



Figure 7: a1) SST (°C) and a2) chlorophyll *a* concentration (mg/m³) from MODIS Aqua on 5th September 2007. The black thick lines represent the filament network. Distance from the coast (km) versus depth profiles of CTD sensors for the EW transect within the filament b) temperature in °C, c) salinity and d) density. Black contours in the salinity section indicates the low salinity plume (< 35.7). The white vertical lines in b) indicate the measurement positions; thick black lines represent the observed bathymetry.



Figure 8: All data are from the NS transect across the tip of the filament at 10.6° W. Latitude versus depth profiles of CTD sensors: a) temperature (°C), b) salinity, c) chlorophyll *a* concentrations from the fluorometer (converted in mg/m³) and d) AOU (µmol/kg). Black contour in c) indicates the maximum of Colored Dissolved Organic Matter measured from another fluorometer. The black dotted line inserted in c) represent the vertically averaged chlorophyll *a* concentrations in the top 50 meters (ranging from 0.35 to 0.55 mg/m³, as indicated on the right y-axis). The white vertical lines in b) indicate the measurement positions; the black rectangles at the surface of a, b, c, d) identify the core of the filament, while the additional one in d) identifies a maximum of AOU under the structure.



Figure 9: Distance from the coast (km) versus depth profiles of chlorophyll *a* concentrations (from fluorometer, converted in mg/m³) along a) EW1 b) EW2 and c) EW within the filament. Black contours on the profile indicate the maximum of AOU concentrations (> 60 μ mol/kg, corresponding roughly to dissolved oxygen concentrations < 200 μ mol/kg). Grey contours close to the surface represent the low salinity plume (< 35.7). The black dotted line on panel c represent the isotherm 16°C. Black dotted rectangles on panel a and b identify the successive upwelling fronts. The thick black lines represent the observed bathymetry.



Figure 10: Distance from the coast (km) versus depth profiles of Nitrate concentrations (from water samples in μ mol/l) along a) EW2 and b) EW within the filament. White markers indicate the measurement positions; white areas are regions where data were too sparse to be robustly interpolated. Black dotted rectangles on panel a identify the successive upwelling fronts. The thick black lines represent the observed bathymetry.



Figure 11: All data are for section EW2 at 40°N. a) Selected phytoplankton pigments surface concentrations from HPLC (0-20 m, two upper panels); b,c) size-fractionated phytoplankton composition (percentage) at the surface (0-20 m) and sub-surface (20-60 m); d) Zooplankton biovolume (size-fractionated) using only the "living objects", as analysed by the Zooscan.



Figure 12: All data are for section EW within the filament. a) Selected phytoplankton pigments surface concentrations from HPLC (0-20 m, two upper panels); b,c) size-fractionated phytoplankton composition (percentage) at the surface (0-20 m) and sub-surface (20-60 m); d) Zooplankton biovolume (size-fractionated) using only the "living objects", as analysed by the Zooscan.

822 References

- Alvarez-Salgado, X., Aristegui, J., Barton, E., Hansell, D., 2007. Contribution of
 upwelling filaments to offshore carbon export in the subtropical Northeast Atlantic
 Ocean. Limnol. Oceanogr. 52, 1287–1292.
- Alvarez-Salgado, X., Castro, C., Perez, F., Fraga, F., 1997. Nutrient mineralization
 patterns in shelf waters of the Western Iberian Upwelling. Cont. Shelf Res. 17,
 1247–1270.
- Alvarez-Salgado, X., Doval, M., Borges, A., Joint, I., Frankignoulle, M., Woodward,
- E., Figueiras, F., 2001. Off-shelf fluxes of labile materials by an upwelling filament in the NW Iberian Upwelling System. Prog. Oceanogr. 51, 321–337.
- Aminot, A., Kerouel, R., 2007. Dosage automatique des nutriments dans les eaux
 marines : méthodes en flux continu. Brest (France). Ed. IFREMER edition.
- Arístegui, J., Barton, E., Alvarez-Salgado, X., Santos, A., Figueiras, F., Kifani,
 S., Hernández-León, S., Mason, E., Machu, E., Demarcq, H., 2009. Sub-regional
 ecosystem variability in the Canary Current upwelling. Prog. Oceanogr. 83, 33–48.
- Barbosa, A., Galvao, H., Mendes, P., Alvarez-Salgado, X., Figueiras, F., Joint, I.,
 2001. Short-term variability of heterotrophic bacterioplankton during upwelling
 off the NW Iberian margin. Prog. Oceanogr. 51, 339–359.
- Barton, E., Arístegui, J., Tett, P., Cantón, M., García-Braun, J., Hernández-León, S.,
- Nykjaer, L., Almeida, C., Almunia, J., Ballesteros, S., Basterretxea, G., Escánez,
- J., García-Weill, L., Hernández-Guerra, A., López-Laatzen, F., Molina, R., Mon-
- tero, M.F., Navarro-Pérez, E., Rodríguez, J., van Lenning, K., Vélez, H., Wild,

- K., 1998. The transition zone of the Canary Current upwelling region. Prog.
 Oceanogr. 41 (4), 455–504.
- Batteen, M., Martinho, A., Miller, H., McClean, J., 2007. A Process-Oriented Study
- of the Coastal Canary and Iberian Current System. Ocean Model. 18, 1–18.
- Batten, S., Fileman, E., Halvorsen, E., 2001. The contribution of microzooplankton
 to the diet of mesozooplankton in an upwelling filament off the north west coast
 of Spain. Prog. Oceanogr. 51, 385–398.
- Borges, A., Frankignoulle, M., 2001. Short-term variations of the partial pressure of CO_2 in surface waters of the Galician upwelling system. Prog. Oceanogr. 51, 283–302.
- Brink, K., Cowles, T., 1991. The Coastal Transition Zone Program. J. Geophys.
 Res. 14, 637–647.
- ⁸⁵⁶ Capet, X., McWilliams, J., Molemaker, M., Shchepetkin, A., 2008. Mesoscale to
 ⁸⁵⁷ Submesoscale Transition in the California Current System. Part I: Flow Structure,
 ⁸⁵⁸ Eddy Flux, and Observational Tests. J. Phys. Oceanogr. 38, 29–43.
- ⁸⁵⁹ Castro, C., Perez, F., Alvarez-Salgado, X., Fraga, F., 2000. Coupling between
 the thermohaline, chemical and biological fields during two contrasting upwelling
 ⁸⁶¹ events off the NW Iberian Peninsula. Cont. Shelf Res. 20, 189–210.
- ⁸⁶² Cermeno, P., Maranon, E., Perez, V., Serret, P., Fernandez, E., Castro, C., 2006.
 ⁸⁶³ Phytoplankton size structure and primary production in a highly dynamic coastal
 ⁸⁶⁴ ecosystem (Ría de Vigo, NW Spain): Seasonal and short-time scale variability.
 ⁸⁶⁵ Estuar. Coast Shelf S. 67, 251–266.

- ⁸⁶⁶ Cravo, A., Relvas, P., Cardeira, S., Rita, F., Madureira, M., Sanchez, R., 2010. An
 ⁸⁶⁷ upwelling filament off southwest Iberia: effect on the chlorophyll a and nutrient
 ⁸⁶⁸ export. Cont. Shelf Res. 30, 1601–1613.
- ⁸⁶⁹ Duró, A., Saiz, E., 2000. Distribution and trophic ecology of Chaetognaths in the
 ⁸⁷⁰ western Mediterranean in relation to an inshoreoffshore gradient. J. Plankton Res.
 ⁸⁷¹ 22, 339–361.
- Fileman, E., Burkill, P., 2001. The herbivorous impact of microzooplankton during
 two short-term Lagrangian experiments off the NW coast of Galicia in summer
 1998. Prog. Oceanogr. 51, 361–383.
- Fiuza, A., Macedo, M., Guerreiro, M., 1982. Climatological space and time variation
 of the Portuguese coastal upwelling. Acta Oecol. 5, 31–40.
- Fréon, P., Barange, M., Arístegui, J., 2009. Eastern Boundary Upwelling Ecosystems:
 Integrative and Comparative Approaches. Prog. Oceanogr. 83, 1–14.
- Garcia, H., Gordon, L., 1992. Oxygen Solubility in Seawater: Better Fitting Equations. Limnol. Oceanogr. 37, 1307–1312.
- García-Munoz, M., Arístegui, J., Pelegrí, J., Antoranz, A., Ojeda, A., Torres, M.,
 2005. Exchange of carbon by an upwelling filament off Cape Ghir (NW Africa).
 J. Marine Syst. 54, 83–95.
- Gasparini, S., 2007.Plankton Identifier: software for a au-884 recognition of planktonic organisms. http://www.obstomatic 885 vlfr.fr/~gaspari/Plankton_Identifier/index.php. 886
- Gorsky, G., Ohman, M., Picheral, M., Gasparini, S., Stemmann, L., Romagnan, J.,
 Cawood, A., Pesant, S., García-Comas, C., Prejger, F., 2010. Digital zooplankton

- image analysis using the ZooScan integrated system. J. Plankton Res. 32 (3),
 285–303.
- Halvorsen, E., Hirst, A., Batten, S., Tande, K., Lampitt, R., 2001. Diet and community grazing by copepods in an upwelled filament off the NW coast of Spain.
 Prog. Oceanogr. 51, 399–421.
- Haynes, R., Barton, E., Pilling, I., 1993. Development, Persistence, and Variability
 of Upwelling Filaments. J. Geophys. Res. 98, 22681–22692.
- Heukelem, L.V., Thomas, C., 2001. Computer-assisted high performance liquid chromatography method development with applications to the isolation and analysis
 of phytoplankton pigments. J. Chromatogr. A 910, 31–49.
- Joint, I., Groom, S., Wollast, R., Chou, L., Tilstone, G., Figueiras, F., Loijens, M.,
 Smyth, T., 2002. The response of phytoplankton production to periodic upwelling
 and relaxation events at the Iberian shelf break: estimates by the ¹⁴C method and
 by satellite remote sensing. J. Marine Syst. 32, 219–238.
- Joint, I., Rees, A., Woodward, M., 2001. Primary production and nutrient assimilation in the Iberian Upwelling in August 1998. Prog. Oceanogr. 51 (2-4), 303–320.
- Labasque, T., Chaumery, C., Aminot, A., Kergoat, G., 2004. Spectrophotometric
 Winkler determination of dissolved oxygen: re-examination of critical factors and
 reliability. Mar. Chem. 88 (1-2), 53–60.
- Landry, M., Calbet, A., 2004. Microzooplankton production in the oceans. ICES
 Mar. Sc. 61, 501–507.
- Landry, M., Ohman, M., Goericke, R., Stukel, M., Barbeau, K., Bundy, R., Kahru,
 M., 2012. Pelagic community responses to a deep-water front in the California

⁹¹² Current Ecosystem: overview of the A-Front Study. J. Plankton Res. 34, 739–
⁹¹³ 748.

- ⁹¹⁴ Lorenzo, L., Arbones, B., Tilstone, G., Figueiras, F., 2005. Across-shelf variability
 ⁹¹⁵ of phytoplankton composition, photosynthetic parameters and primary production
 ⁹¹⁶ in the NW Iberian upwelling system. J. Marine Syst. 54, 157–173.
- Meunier, T., Rossi, V., Morel, Y., Carton, X., 2010. Influence of a bottom topography
 on an upwelling current: generation of long trapped filaments. Ocean Model. 35,
 277–303.
- Motoda, S., 1959. Devices of simple plankton apparatus. Hokkaido University,
 Japan.. Faculty of Fisheries. edition.
- Otero, P., Ruiz-Villarreal, M., Peliz, A., 2008. Variability of river plumes off Northwest Iberia in response to wind events. J. Marine Syst. 72, 238–255.
- Pauly, D., Christensen, V., 1995. Primary production required to sustain global
 fisheries. Nature 374, 255–257.
- Peliz, A., Dubert, J., Santos, A., Oliveira, P., Cann, B.L., 2005. Winter upper ocean
 circulation in the Western Iberian Basin Fronts, Eddies and Poleward Flows: an
 overview. Deep-Sea Res. Pt I 52, 621–646.
- Peliz, A., Rosa, T., Santos, A., Pissarra, J., 2002. Fronts, jets, and counter-flows in
 the Western Iberian upwelling system. J. Marine Syst. 35, 61–77.
- Quaresma, L., Vitorino, J., Oliveira, A., da Silva, J., 2007. Evidence of sediment
 resuspension by non-linear internal waves on the western Portuguese mid-shelf.
 Mar. Geol. 246, 123–143.

- ⁹³⁴ Queiroga, H., Silva, C., Sorbe, J., Morgado, F., 2005. Composition and distribution
- of zooplankton across an upwelling front on the northern Portuguese coast during
- ⁹³⁶ summer. Hydrobiologia 545, 195–207.
- 937 Raimund, S., Quack, B., Bozec, Y., Vernet, M., Rossi, V., Morel, Y., Garçcon, V.,
- Morin, P., 2011. Sources of short-lived bromocarbons in the Iberian upwelling system. Biogeosciences 8, 1551–1564.
- Ras, J., Claustre, H., Uitz, J., 2008. Spatial variability of phytoplankton pigment
 distributions in the Subtropical South Pacific Ocean: comparison between in-situ
 and predicted data. Biogeosciences 5, 353–369.
- Relvas, P., Barton, E., Dubert, J., Oliveira, P., Peliz, A., da Silva, J., Santos, A.,
 2007. Physical oceanography of the western Iberia ecosystem: Latest views and
 challenges. Prog. Oceanogr. 74, 149–173.
- Resende, P., Azeiteiro, U., Goncalves, F., Pereira, M., 2007. Distribution and ecological preferences of diatoms and dinoflagellates in the west Iberian Coastal zone
 (North Portugal). Acta Oecol. 32, 224–235.
- Ribeiro, A., Peliz, A., Santos, A., 2005. A study of the response of chlorophyll-a
 biomass to a winter upwelling event off Western Iberia using SeaWiFS and in-situ
 data. J. Marine Syst. 53, 87–107.
- Roed, L., Shi, X., 1999. A numerical study of the dynamics and energetics of cool
 filaments, jets and eddies off the Iberian Peninsula. J. Geophys. Res. 104, 29817–
 29841.
- ⁹⁵⁵ Rossi, V., 2010. Influence of mesoscale physical processes on planktonic ecosystems

⁹⁵⁶ in the regional ocean: application to the Eastern Boundary Upwelling Systems.

- Ph.D. thesis. Université of Toulouse III Paul Sabatier / LEGOS, Toulouse, France.
- Rossi, V., Morel, Y., Garçon, V., 2010. Effect of the wind on the shelf dynamics:
 formation of a secondary upwelling along the continental margin. Ocean Model.
 31 (3-4), 51–79.
- Sanchez, R., Relvas, P., Martinho, A., Miller, P., . Physical description of an upwelling filament west of Cape St. Vincent in late october 2004 .
- Santos, A., Chícharo, A., dos Santos, A., Moita, T., Oliveira, P., Peliz, A., Ré, P.,
 2007. Physical-biological interactions in the life history of small pelagic fish in the
 Western Iberia Upwelling Ecosystem. Prog. Oceanogr. 74, 192–209.
- Tilstone, G., Figueiras, F., Lorenzo, L., Arbones, B., 2003. Phytoplankton composition, photosynthesis and primary production during different hydrographic
 conditions at the Northwest Iberian upwelling system. Mar. Ecol-Prog. Ser. 252,
 89–104.
- Torres, R., Barton, E., 2007. Onset of the Iberian upwelling along the Galician coast.
 Cont. Shelf Res. 27, 1759–1778.
- Varela, R., Roson, G., Herrera, J., Torres-Lopez, S., Fernandez-Romero, A., 2005.
 A general view of the hydrographic and dynamical patterns of the Rías Baixas
 adjacent sea area. J. Marine Syst. 54, 97–113.