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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 (~ 40 % of the length of the front) are responsible of a greater offshore transport of chlorophyll (~ 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. Introduction

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

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 wind-driven 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.

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

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

41 A quasi-meridional upwelling front develops between the cold recently upwelled
42 enriched waters at the coast and warmer oligotrophic offshore waters. This strong
43 cross-shore temperature gradient, itself related to the ambient nutrient concentra-
44 tions, is indeed strongly influencing the phytoplankton assemblages (Resende et al.,
45 2007). Tilstone et al. (2003) and Lorenzo et al. (2005) also described the coastal
46 upwelling communities as microplankton dominated, whereas mainly cyanobacteria
47 (picoplankton) are found in the oceanic waters.

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

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

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

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

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

92 **2. Materials and methods.**

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

94 The MOUTON07 cruise was conducted along the western coast of the Iberian
95 Peninsula (mainly Portuguese coast), onboard the Research Vessel R/V "Pourquoi-
96 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 14th to August 25th and then
100 from August 30th to September 9th, 2007 (see Fig. 1).

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

110 *2.2. Bio-physical sensors and water sampling.*

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

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

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

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

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

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

145 The oxygen probe was calibrated by independent sampling and Winkler titration
146 following Labasque et al. (2004) (and references therein). The calibration samples
147 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).

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

154 *2.3. Biogeochemical and biological sampling.*

155 *2.3.1. Dissolved nutrients.*

156 The seawater samples collected onboard for nutrient analysis were stored at
157 -20°C for later analysis. The common nutrients concentrations - namely nitrate
158 + nitrite, silicate and phosphate - were then determined in the labs (on land) by
159 colorimetric methods using an Technicon Autoanalyser II, following the protocols
160 and methods described in Aminot and Kerouel (2007).

161

162 *2.3.2. Phytoplanktonic pigments.*

163 The water samples for photoactive pigments analysis were collected at 2 or 3
164 depths and then were vacuum filtered through 25 mm diameter Whatman GF/F
165 fiber glass filters (0.7 μm particle retention size). Filtered volumes varied between
166 3 l in the offshore waters and less than 1l for some stations inside the coastal
167 upwelling zone. The filters were immediately stored in liquid nitrogen until analysis
168 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.

170 Phytoplankton pigments composition was determined by High Performance Liq-
171 uid Chromatography (HPLC) methods. The filters were extracted and then rapidly
172 analysed (within 24 h) by HPLC with a complete Agilent Technologies system. Fol-
173 lowing an adaptation of the method described by Heukelem and Thomas (2001),
174 the concentrations (in mg/m³) of 13 separate phytoplankton pigments (see Tab.
175 1) were calculated from the absorption spectra with an internal standard correc-
176 tion and external calibration. With a lower limit of detection for chlorophyll *a* of
177 0.0001 mg/m³ and an injection precision of 0.4 %, the accuracy of this method has
178 been largely proven (Ras et al., 2008). Additional pigments as phaeophorbide *a*
179 (*phaeo-a*), chlorophyllide *a* (*chloid-a*) and divinyl chlorophyll *a* (*div-chlo-a*) were
180 measured only on a subset of the total samples.

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

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.*

193 Zooplankton samples were collected during day and night at one CTD station out
194 of two or three, with the highest possible frequency. A WP2 plankton net (mouth
195 surface of 0.25 m²) mounted with 200 µm mesh size was used, and towed vertically at
196 around 1 m/s over the water column from 5 m above the sea floor, or 70 m depth, up
197 to the surface. The proper volume of water filtered was calculated using the effective
198 depth of the tow as measured by a cable meter. The sample was then splitted into two
199 fractions using a motoda box (Motoda, 1959) and a fraction was directly preserved
200 in formaldehyde for later digitalisation, whereas the other half sample was fixed on
201 a pre-weighted filter (200 µm) and conserved at −20°C in individual sterile cases.

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

217 were used whereas equivalent spherical diameter (ESD) was used for other organisms
218 (Gorsky et al., 2010). Finally, two classes of size were defined by a limit volume of
219 1 mm^3 that represent the small (Ciliates / small Copepods) and large individuals
220 (large Copepods, Chaetognaths, meroplankton...) found in the area. Although the
221 common criteria to differentiate micro- and meso- zooplankton is the body length,
222 this biovolume approach is in accord with their distinct ecological function (Gorsky
223 et al., 2010).

224 **3. Results and Discussion.**

225 *3.1. Meteorological conditions.*

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

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

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

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

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

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

260 A typical upwelling circulation can be identified along every zonal section, al-
261 though other mechanisms (internal waves or vortices) certainly superimpose their
262 dynamical signature. The typical upwelling circulation is especially marked dur-
263 ing leg 1 when the favourable winds were very strong (i.e. EW1 section, Fig. 4a).
264 Along-shore velocities are mostly southward, intensified at the surface, ranging from
265 -0.1 to -0.15 at the sub-surface to ~ -0.25 m/s or more at the surface (Fig. 4a2).

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

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

287 At the inner shelf, these along-shore alternating flows resulted in a convergence
288 zone at the base of the filament ($9.5^\circ\text{W} / 40.3^\circ\text{N}$) and are consistent with the pres-
289 ence of a dipole, with a cyclonic mesoscale eddy on the northern part (EW1) and
290 an anticyclonic one further south (EW2), promoting the extension of the filament.
291 Sanchez et al. also documented the contribution of strong opposing subsurface flows

292 to the generation of filaments at their base. Away from the coast (40-70 km), the
293 filamental structure is associated with a strong offshore current in the surface layer
294 and an onshore current below (Fig. 5a1), consistent with the westward extension of
295 the filament (Fig. 3a and Fig. 7a).

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

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

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

332 *3.3. Cross-shore physical variability.*

333 *3.3.1. Description of the successive upwelling fronts.*

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

343 $S \geq 35.7$. Another specific upwelling front is located between 30-50 km, with again
344 clear salinity, temperature and density fronts. It may correspond to a previous wind
345 pulse that occurred 5-8 days ago. Other frontal features, such as the one identified
346 between 65-75 km from the coast, could either correspond to even older upwelling
347 events (10-15 days) or mesoscale features. The lighter and warmer surface waters
348 ($\sigma_\theta < 26.2$) are pushed offshore (further than 80 km) by the Ekman drift associated
349 with the equatorward winds.

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

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

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

373 Another feature of interest is the low salinity surface plume (≤ 35.7) observed
374 between 20 and 80 km from the coast at 41°N (EW1, Fig. 6a) whose origin is unclear.
375 Low salinity waters are also found just above the seabed, indicating a possible origin
376 from the deep slope waters (ENACWsp > 150 m) being upwelled onto the shelf.
377 Another possible explanation is the influence of the WIBP ($S < 35.7$) (Peliz et al.,
378 2002) at the northern tip of the IPUS, related to the freshwater discharge from the
379 Galician Rias and Northern Portuguese rivers (the most significant discharges being
380 from the Minho and Douro rivers). However, because of the moderate freshwater
381 input during the upwelling season, the low salinity signal might indeed originate
382 from both the moderate rivers' input mixed with the recently upwelled ENACWsp.

383 Interestingly, the low salinity plume is observed at 40°N (EW2, Fig. 6b) between
384 45 and 80 km, further offshore than along EW1 (Fig. 6a). The thickness of this layer
385 of less saline water ($\sim 30\text{-}40$ m) is maintained during its south-westward drift by the
386 PC/PCC. However its width had decreased from 60 (EW1) to 35 km (EW2). Otero
387 et al. (2008) studied the dynamics and extension of this low salinity lens, showing
388 that it is highly influenced by the wind regime and the shelf circulation (i.e. PCC and
389 IPC). The freshwater plume is confined at the coast when poleward winds prevail,
390 whereas it is exported offshore and southward under upwelling favourable wind, as it
391 is the case here. Some studies also emphasized the crucial role this physical feature
392 has on the biological activity, from plankton (Ribeiro et al., 2005) to fish recruitment
393 (Santos et al., 2007).

394 *3.3.2. Structure of the mesoscale filament.*

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

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

417 The low salinity tongue (< 35.7), possibly originating from the coast, is also ob-
418 served within the filament (Fig. 7b). Likely to be composed of the WIBP mixed

419 with the ENACWst/sp recently upwelled, these "fresh" waters have been advected
420 inside the filament up to 140 km offshore (against 80 km for the EW section). Con-
421 sistently, the meridional section across the tip of the structure (Fig.8b) revealed a
422 salinity minimum. All our observations agree with Peliz et al. (2002) and suggest
423 that the characteristics of the filament (buoyant waters in its core and the presence
424 of mesoscale eddies at its tips) favour a preferential conduct for exchanges between
425 coastal and offshore waters.

426 *3.4. Contrasting biological responses.*

427 *3.4.1. Chlorophyll a distribution from the fluorometer.*

428 The general satellite-derived chlorophyll *a* pattern shows maximal concentrations
429 of 1 – 10 mg/m³ at the coast, while the offshore waters are relatively poor ~ 0.1
430 mg/m³ or less (Fig. 3a2, b2). These two sub-domains are sharply delimited by the
431 upwelling front at ~ 150 km off the coast, while mesoscale filaments with moder-
432 ate surface chlorophyll *a* concentration (0.1 – 1 mg/m³) extend up to ~ 200-300
433 km offshore.

434 The successive upwelling fronts examined previously along both EW transects
435 (section 3.3.1) are marked with a local surface maxima in chlorophyll *a*, almost
436 equally distributed from the surface down to 30-40 m (Fig. 9a, b). These fronts
437 gradually advected offshore have been analysed by Rossi et al. (2010) along EW1
438 and are also observed along EW2 (Fig. 9b). The most recent upwelling event is
439 characterized by high chlorophyll *a* concentrations (1 – 3 mg/m³) within 20 km from
440 the coast, then comes the previous one between 30 and 50 km supporting the highest
441 chlorophyll concentrations (1 – 10 mg/m³). The maximum response of the ecosystem
442 in terms of chlorophyll *a* is found over the mid-shelf, developing shortly (about 5-8
443 days) after the initial upwelling pulse. Finally the most ancient front is found offshore

444 between 65 and 75 km with moderate chlorophyll *a* content ($0.3 - 1 \text{ mg/m}^3$) some
445 10 to 15 days after the pulse. The ancient front along EW1 also concerns similar
446 chlorophyll *a* concentrations ($0.5 - 1 \text{ mg/m}^3$) and extends until 85 km against 75
447 km for EW2, which correspond to a westward drift of about 10 km during 3 days.
448 Note that the coastal areas ($< 20 \text{ km}$) along EW1 are quite poor in chlorophyll
449 *a* probably due to the fact that the sampling was carried out exactly during the
450 upwelling pulse.

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

459 Waters westward of the most ancient front ($> 80 \text{ km}$) are characterized by a
460 deeper SCM ($\sim 50\text{-}70 \text{ m}$) of lower chlorophyll *a* concentrations ($< 0.5 \text{ mg/m}^3$) and
461 poor surface waters ($< 0.1 \text{ mg/m}^3$).

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

470 within the filament until 160 km offshore, extending considerably (more than 100 km)
471 the surface of biologically productive waters as compared to EW1 and EW2 (85 and
472 75 km respectively). Even across the tip of the structure (Fig. 8c), chlorophyll *a*
473 concentrations are higher within the filament ($0.3 - 1 \text{ mg/m}^3$) than outside ($0.1 - 0.3$
474 mg/m^3).

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

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.

491 It is worth noting that the minimum of dissolved oxygen ($< 200 \text{ } \mu\text{mol/kg}$),
492 corresponding to a maximum of AOU ($> 60 \text{ } \mu\text{mol/kg}$) is found on the shelf bottom,
493 while its lateral position coincides very well with the highest surface concentrations
494 of chlorophyll *a* (see black isolines on Fig. 9a, b, c). It is a sign of an intense *in-*

495 *situ* consumption of oxygen by the microbial remineralisation of the sinking organic
496 matter.

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

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

521 3.4.3. Dissolved Nutrients.

522 Nutrient concentrations in the mixed layer (down to 40 m) within the most re-
523 cently upwelled waters (less than 30 km from the coastline) range around 10 – 12
524 $\mu\text{mol/l}$ for nitrate (Fig.10a), $\sim 1 \mu\text{mol/l}$ for phosphate and $\sim 6 \mu\text{mol/l}$ for silicate
525 (not shown). Cravo et al. (2010) compiled several nutrients values from the litera-
526 ture and our values are found in the upper range of their dataset, attesting of the
527 strong upwelling event sampled. Then, in the former upwelling front (30-50 km),
528 they decrease down to 2 – 5 $\mu\text{mol/l}$, 0 – 0.4 $\mu\text{mol/l}$ and 1 – 2 $\mu\text{mol/l}$ for nitrate,
529 phosphate and silicate respectively. Finally, more than 65 km from the coast, the ni-
530 trate concentration are below detection levels, whereas low concentrations of silicate
531 (0.3 – 0.7 $\mu\text{mol/l}$) and phosphate (0.1 $\mu\text{mol/l}$) remain (not shown). This gradual nu-
532 trient depletion, similarly observed along EW1 (not shown) and within the filament
533 (Fig.10b), is likely to be due to constant phytoplankton uptake along the westward
534 drift of the freshly upwelled waters. The absence of nitrate offshore while silicate and
535 phosphate are still detectable reinforces the fact that nitrate is the limiting factor
536 for primary production in surface waters (Castro et al., 2000; Joint et al., 2001).
537 Another hypothesis that could explain this excess of silicate and phosphate is their
538 preferential remineralisation rate revealed by Alvarez-Salgado et al. (1997).

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 $\mu\text{mol/l}$ 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*

546 remineralisation of organic matter originating from the surface biological production.

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

554 *3.5. Comparative analysis of the planktonic communities.*

555 *3.5.1. Phytoplankton communities.*

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

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

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

596 The pigments concentration from HPLC can also provide broad information about

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

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

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

630 Similar conclusions about the phytoplankton assemblages can be drawn from the
631 planktonic community of the filament (Fig. 12a), although some differences remain.
632 In particular, the total chlorophyll *a* (HPLC) is still significant 150 km offshore with
633 0.8 mg/m³, whereas it was below 0.1 mg/m³ from 70 km along the EW sections,
634 strengthening the results from sect. 3.4.1. Although diatoms and dinoflagellates
635 are present above the shelf, the dinoflagellate population seems larger than along
636 EW2 (up to 0.15 mg/m³ of *peri* in the filament against 0.05-0.1 mg/m³ along EW2).
637 When moving offshore, these large cells are replaced by smaller ones: cyanobacte-
638 ria, prochlorophytes (*zea*, *div-chlo-a*) and prymnesiophytes (*19-hex*) increase rapidly
639 (Fig. 12a). Another significant difference is the concentration of *19-hex*: it is 0.25
640 mg/m³ until 150 km offshore within the filament but \leq 0.1 mg/m³ along EW2 from
641 70 km). These pico- and nano-phytoplankton dominate the communities within
642 the filament, in line with Barbosa et al. (2001) who found that bacterioplankton is
643 around 15 % of the total plankton community production over the shelf, whereas it
644 can reach about 40 % under more oligotrophic conditions in a filament.

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

648 *3.5.2. Zooplanktonic biomasses.*

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

656 Large individuals dominate from 30 to 50 km (Fig. 11d and Fig. 12d) and con-
657 stitute a "transitional" community. Zooplankton groups such as Oithona Copepods,
658 Chaetognaths, Bryozoan larvae, Bivalves and Appendicularians prevail there. The
659 presence of Bryozoan larvae (meroplankton released by neritic benthic adults) at
660 the mid- and outer-shelf suggests that this zooplankton community originated from
661 the coastal upwelling and have then been gradually exported offshore, in line with
662 our previous analysis (sect. 3.3 and 3.5.1). The presence of Chaetognaths, preda-
663 tors of Copepods (Duró and Saiz, 2000), indicates the establishment of a mature
664 zooplankton community with secondary consumers trophic levels. Within 15 – 60
665 km from the coast, the micro-phytoplankton, especially diatoms (Fig. 11a, red line),
666 responds quickly (2-4 days) to the successive upwelling pulses and dominates the
667 shelf assemblages. These high levels of microphytoplankton biomass may contribute
668 to sustain the longer development of the large zooplankton organisms during their
669 offshore drift, explaining why they dominate only from ~ 30 km (i.e. about 5-10
670 days after the initial pulse). This is in good agreement with Queiroga et al. (2005)
671 who also documented the apparition of both meroplankton and planktonic preda-
672 tors during the offshore displacement of a coastal zooplanktonic community in the

673 upwelling season.

674 Note that large zooplankton organisms are still observed as far as 150 km offshore
675 within the filament ($\sim 100 \text{ mm}^3/\text{m}^3 \text{ BV}$, Fig. 12d), whereas they were completely
676 absent from 70 km along EW2 (Fig. 11d). the frontal structure (EW1, EW2) seems
677 to strongly isolate large zooplankton individuals from the open ocean (Landry et al.
678 (2012) and references therein), so that the location of the upwelling front (itself
679 driven by the successive pulses of equatorward winds) may set the maximal offshore
680 extension of these large organisms which are an important food source for exploited
681 higher trophic levels. Unfortunately, the lack of sampling at high spatial resolution
682 near the physical boundary does not allow us to conclude firmly. It also shows that
683 the "transitional" community drift further offshore and thus develop a longer time
684 within the filament than along the EW1/EW2 transect, where it is confined between
685 the mid-shelf and the most offshore upwelling front ($\sim 70 \text{ km}$).

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

694 The offshore oligotrophic ecosystem is characterized by low biomass of small
695 organisms ($> 70 \text{ km}$ for EW2 on Fig. 11d and $> 160 \text{ km}$ for the filament on
696 Fig. 12d), essentially composed of $\sim 50 \%$ of small Copepods and $\sim 50 \%$ of
697 Cladocera (not shown). In the open ocean (offshore the main front and outside the
698 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.*

701 In this section, we calculate estimates of offshore transport and chlorophyll fluxes
702 through the filament and across the upwelling front based on a typical situation of the
703 north-western Iberian margin during upwelling season (see Fig. 3b1). The upwelling
704 front extends meridionally from $\sim 37^\circ\text{N}$ to $\sim 43.5^\circ\text{N}$ (720 km) and is interrupted
705 by four large filaments. In approximation, the system can thus be separated into
706 4 filaments, each having about 70 km width, and a more regular quasi-meridional
707 semi-continuous front extending over 440 km.

708 The currents derived from the LADCP at 10.6°W (see Fig. 5b) allow us to
709 evaluate the offshore transport induced by the filament at its tip. Using the horizontal
710 boundaries from 40.3° to 40.45°N with a vertical extension of 50 m, a westward
711 transport of ~ 0.16 Sv due to the filament is estimated. This falls within the lower
712 range of the compilation of observations of upwelling filaments by Sanchez et al.,
713 probably because the transport is computed at the tip of the filament. By multiplying
714 the westward velocities by the chlorophyll content (averaging to 0.55 mg/m³), a flux
715 of chlorophyll of around 0.016 mg m⁻² s⁻¹ is obtained. Integrating this value over
716 its cross-section (50 m for 0.15° of latitude) yields to about 82.5 g/s of chlorophyll
717 *a* transported offshore at the tip of the filament, in very good agreement with the
718 flux of 70.7 g/s calculated by García-Munoz et al. (2005) in the Canary upwelling
719 system.

720 To approximate the cross-shore transport of near-coastal water masses due to
721 this structure, we consider the westward velocities recorded at the tip of the filament
722 as similar to the ones during its initiation (~ 0.11 m/s). In addition, we integrate
723 Chlorophyll *a* concentrations from the coastal areas (~ 1 mg/m³) over the dimensions

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

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

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

750 4. Conclusions.

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

756 Our analysis emphasized the role of mesoscale features such as eddies and fila-
757 ments that superimpose their dynamical signature on the classical upwelling flow.
758 Nevertheless, surface velocities often directed to the west produce a significant off-
759 shore transport through the meridional upwelling front. This transport is intensified
760 within the filament surveyed due to the presence of mesoscale dipolar eddies at the
761 base and tip of the elongating structure.

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

769 Composed of the recently upwelled ENACW mixed with the WIBP, low salinity
770 waters provide a buoyancy input to the filamental structure promoting its offshore
771 elongation. In contrast with EW sections, the water is relatively homogeneous within
772 the 3 dimensional filamental structure but well isolated from the surrounding. The
773 resulting biological response is organised as a shallower subsurface maximum ex-
774 tending far offshore (up to 160 km). High surface chlorophyll *a* concentrations are

775 associated with low oxygen levels at the subsurface, a sign of nutrient remineralisa-
776 tion processes that are favoured below the filament.

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

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

800 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
<i>Chlorophyll a</i>	<i>chlo-a</i>	All	All - except Prochlorophytes
<i>Chlorophyll b</i>	<i>chlo-b</i>	P + N	Green algae (Chlorophytes, Prasinophytes)
<i>Peridinin</i>	<i>peri</i>	M	Dinoflagellates
<i>Fucoxanthin</i>	<i>fuco</i>	M	Diatoms , Prymnesiophytes, and some Dinoflagellates
<i>Zeaxanthin</i>	<i>zea</i>	P	Cyanobacteria, Prochlorophytes
<i>Alloxanthin</i>	<i>allo</i>	P + N	Cryptophytes
19 – <i>Butanoyloxyfucoxanthin</i>	<i>19-but</i>	N	Prymnesiophytes, Pelagophytes
19 – <i>Hexanoyloxyfucoxanthin</i>	<i>19-hex</i>	N	Prymnesiophytes (Haptophytes)
<i>Divinyl Chlorophyll a</i>	<i>div-chlo-a</i>	P	Prochlorophytes
<i>Chlorophyllide a</i>	<i>chloid-a</i>	-	Senescent diatoms
<i>Phaeophorbide a</i>	<i>phaeo-a</i>	-	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.

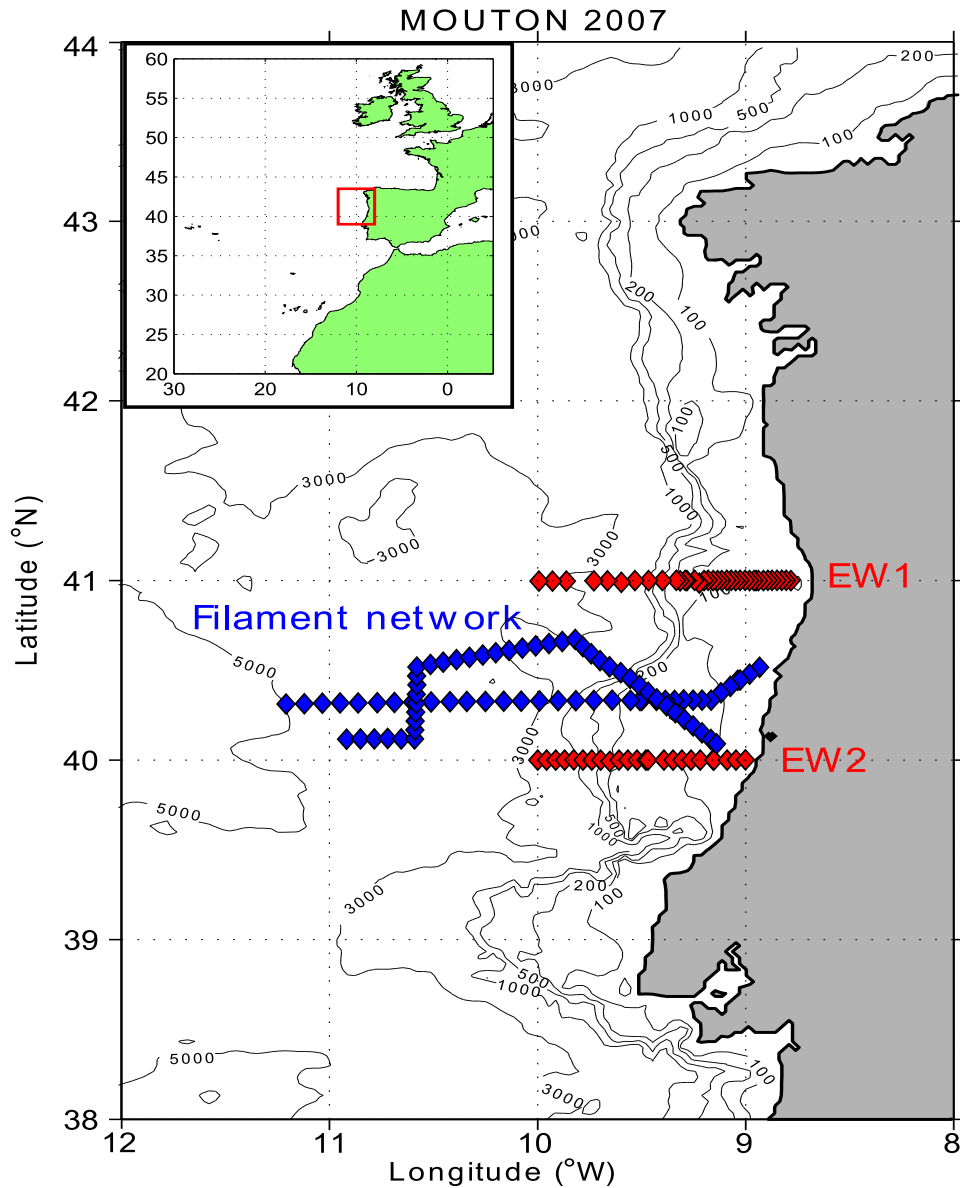


Figure 1: Overview of the MOUTON 2007 oceanographic campaign in the Iberian Peninsula Upwelling System. Colored diamonds represent the CTD stations organised as transects (red for East-West sections: EW1 at 41° and EW2 at 40°; blue for the filament network). Black contours represent the bathymetry (in 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.

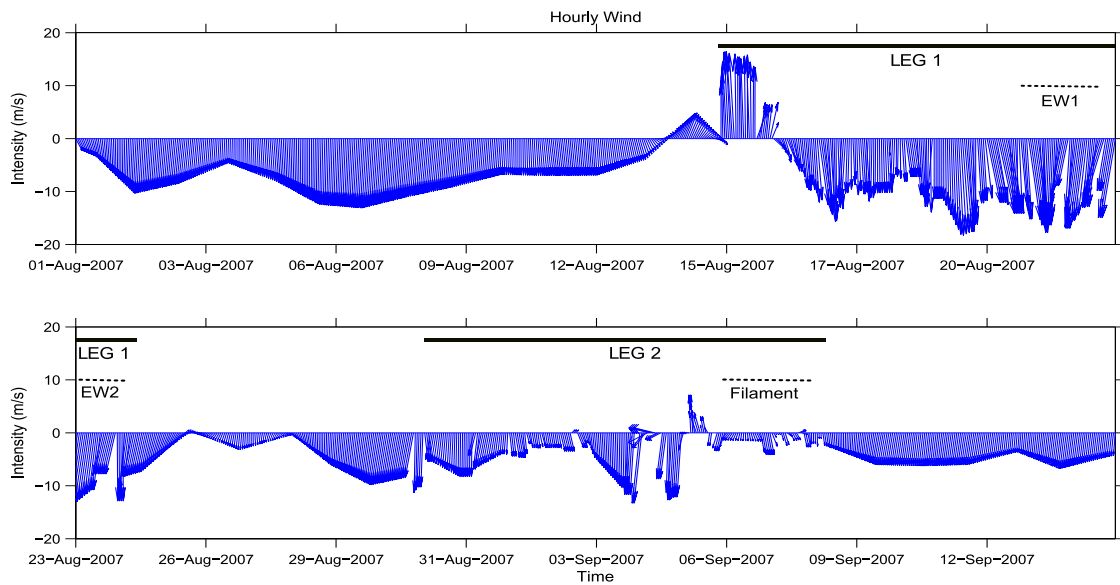


Figure 2: Wind (in m/s) vectors from the QuikSCAT scatterometer (averaged over the surveyed area $39 - 43^{\circ}N / 9 - 12^{\circ}W$) and the onboard measurements (during both legs of the survey, as shown by the black segments). Black dotted segments indicate when the transects of interest were carried 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.

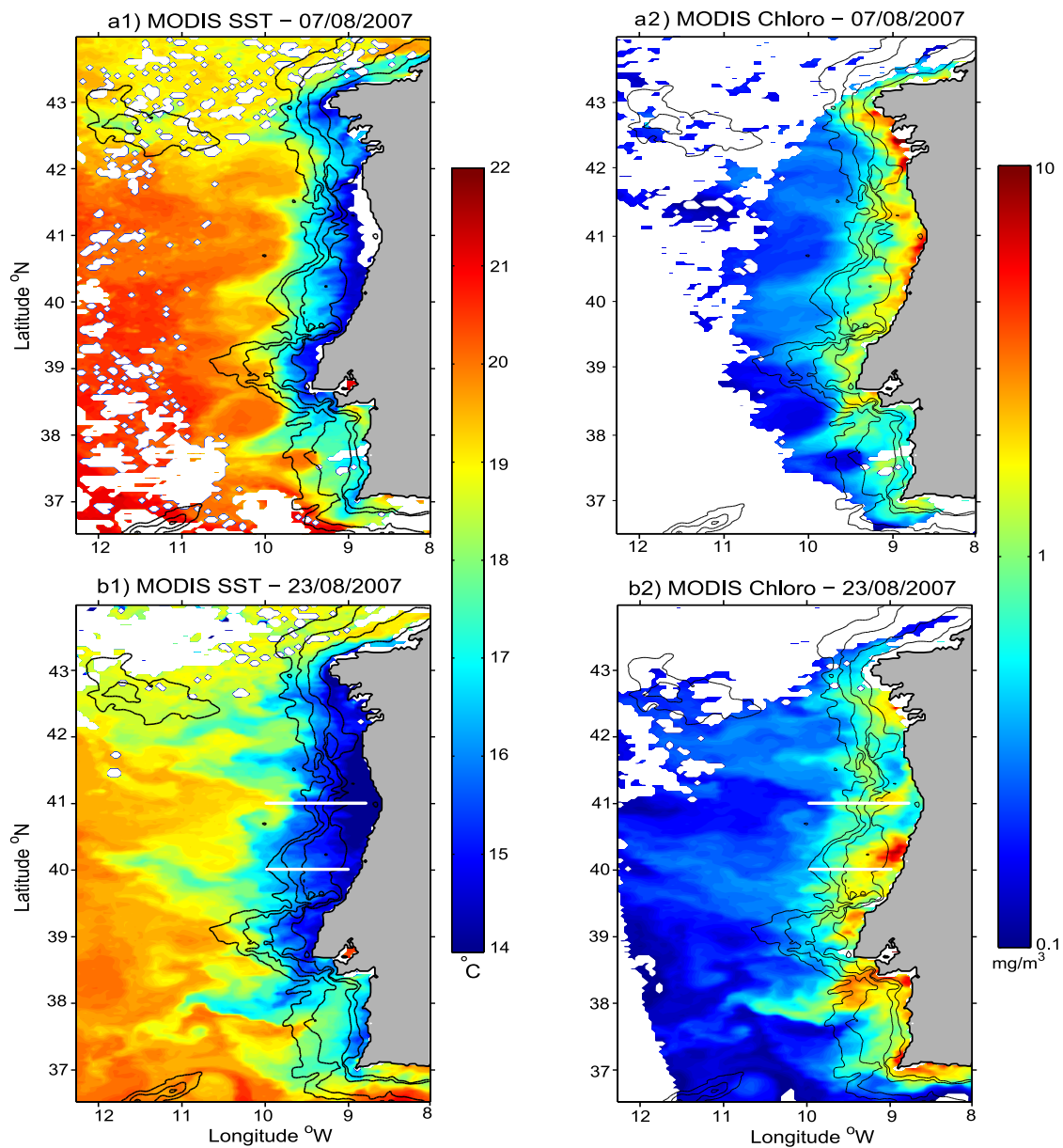


Figure 3: Daily Sea Surface Temperature ($^{\circ}\text{C}$) and Chlorophyll-*a* (mg/m^3) from MODIS Aqua for a) 7th August 2007 and b) 23rd August 2007. White areas are clouds and black contours represent the bathymetry (200, 500, 1000 and 2000 m). On lower panels b1) and b2), the white segments represent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

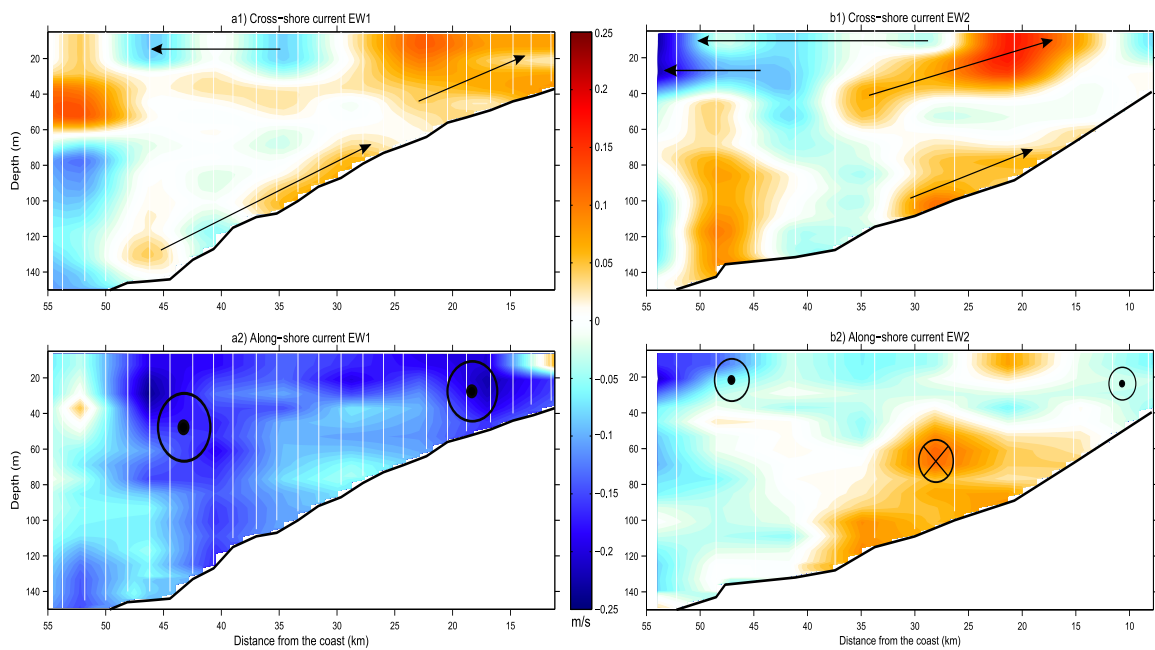


Figure 4: Cross-shore (a1, b1) and along-shore (a2, b2) velocities (m/s) derived from the LADCP along EW1 at 41°N (a) and EW2 at 40°N (b). On the upper panels blue color indicates westward/offshore current and red color eastward/onshore. On the lower panels, red color represent northward current and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

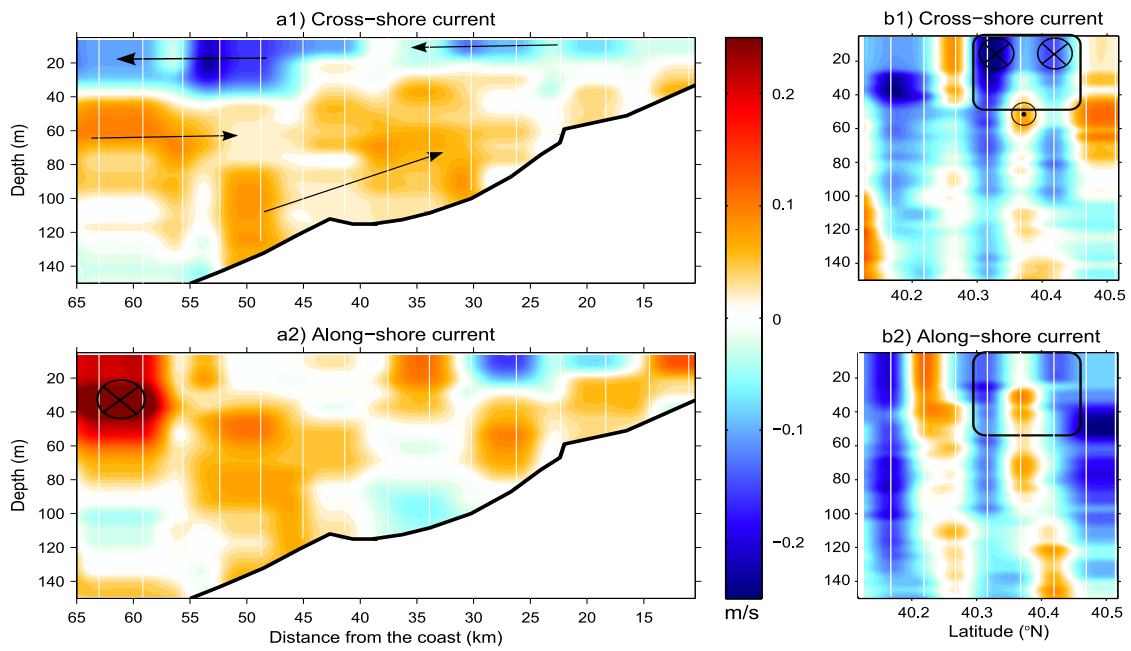


Figure 5: Cross-shore (a1, b1) and along-shore (a2, b2) velocities (m/s) derived from the LADCP along the East-West transect within the filament (a) and the North-South section across its tip at 10.6° W (b). On the upper panels blue color indicates westward/offshore current and red color eastward/onshore. 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.

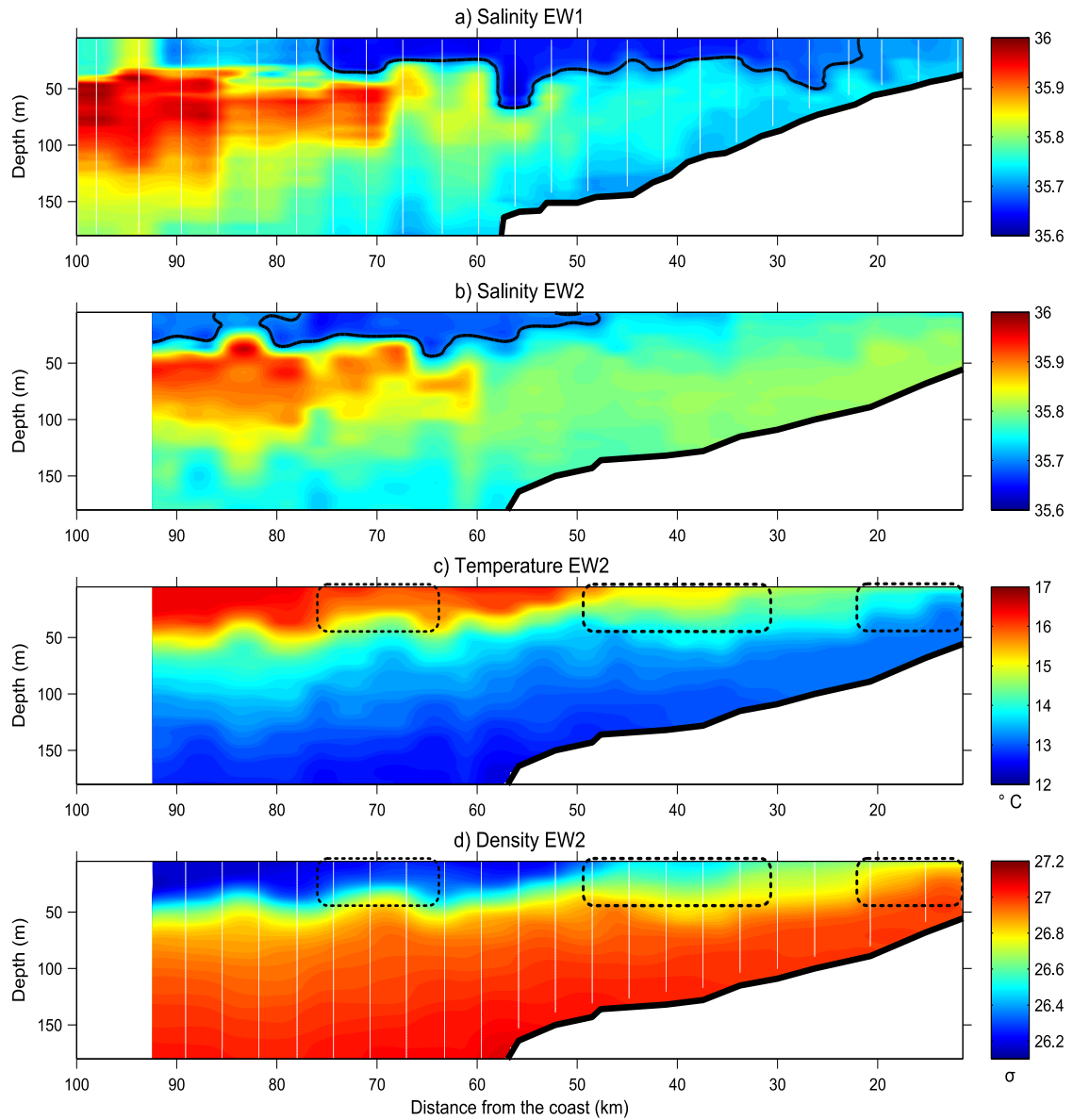


Figure 6: Distance from the coast (km) versus depth profiles of CTD sensors along both cross-shore transects. a) EW1 salinity; b) EW2 salinity, c) temperature ($^{\circ}\text{C}$) and d) density (σ_{θ}). The black lines in the salinity sections contour the low salinity plume (< 35.7). The white vertical 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.

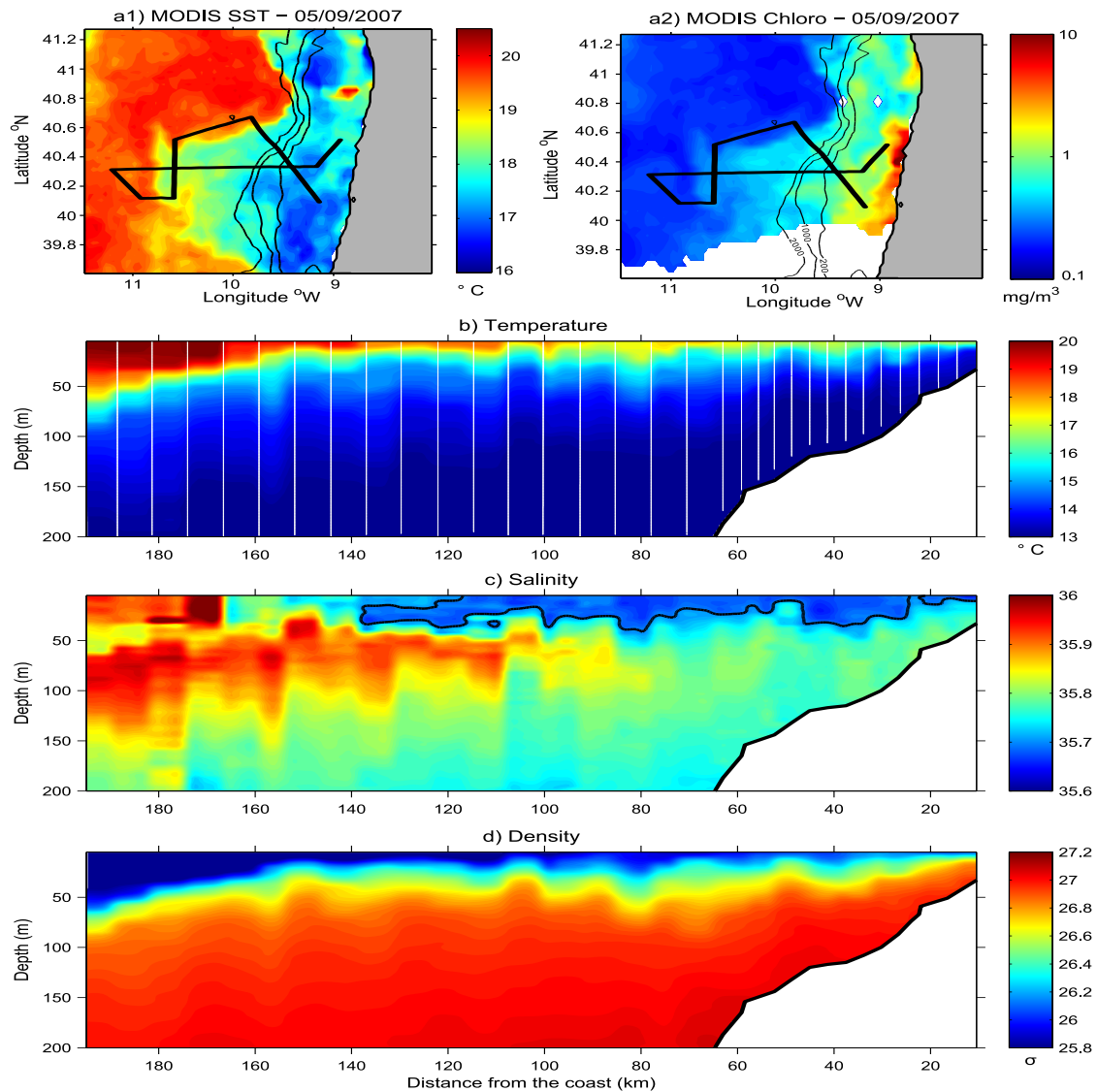


Figure 7: a1) SST ($^{\circ}\text{C}$) and a2) chlorophyll *a* concentration (mg/m^3) from MODIS Aqua on 5th September 2007. The black thick lines represent the filament network. Distance from the coast (km) versus depth profiles of CTD sensors for the EW transect within the filament b) temperature in $^{\circ}\text{C}$, 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.

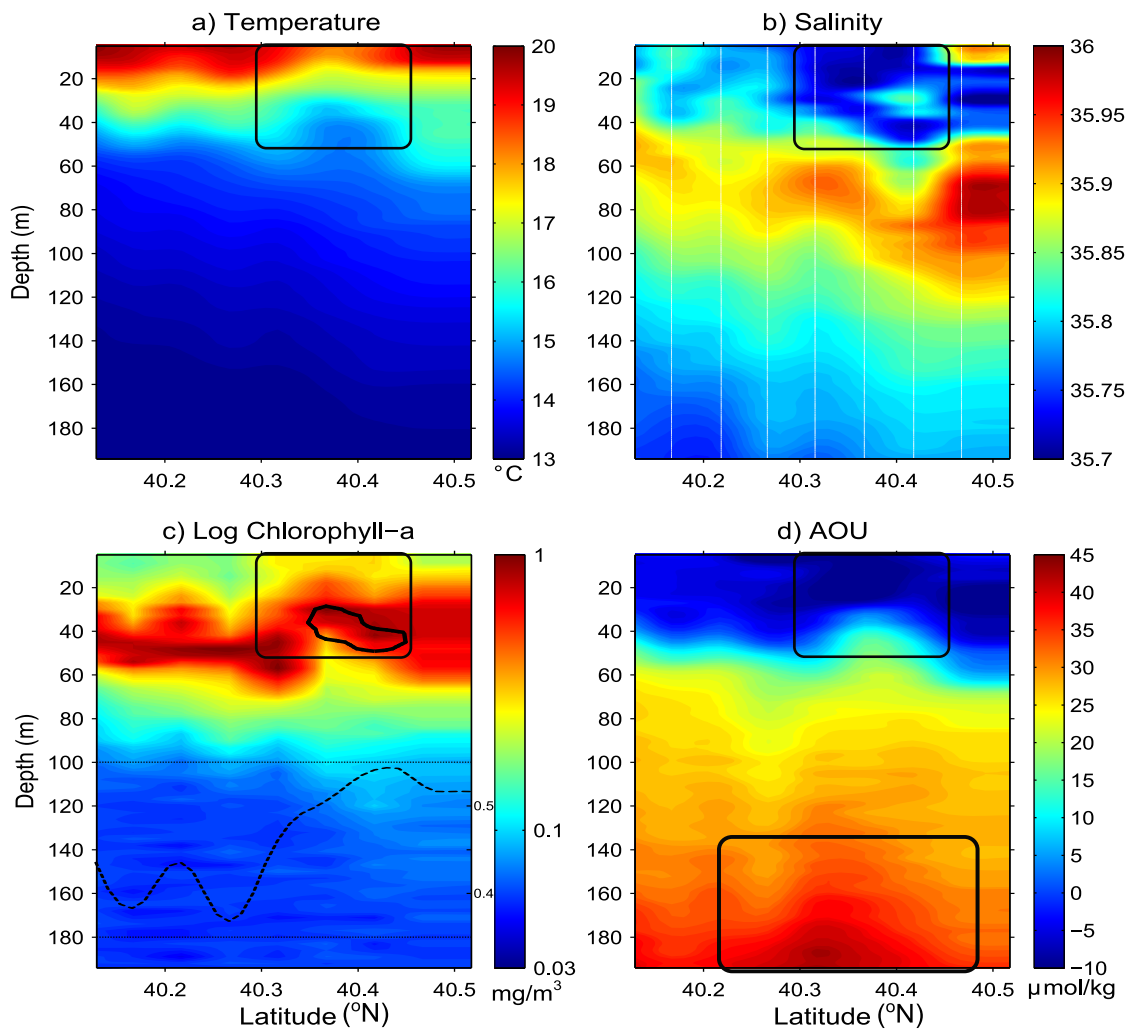


Figure 8: All data are from the NS transect across the tip of the filament at 10.6°W. Latitude versus depth profiles of CTD sensors: a) temperature (°C), b) salinity, c) chlorophyll *a* concentrations from the fluorometer (converted in mg/m³) and d) AOU (μmol/kg). Black contour in c) indicates the maximum 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.

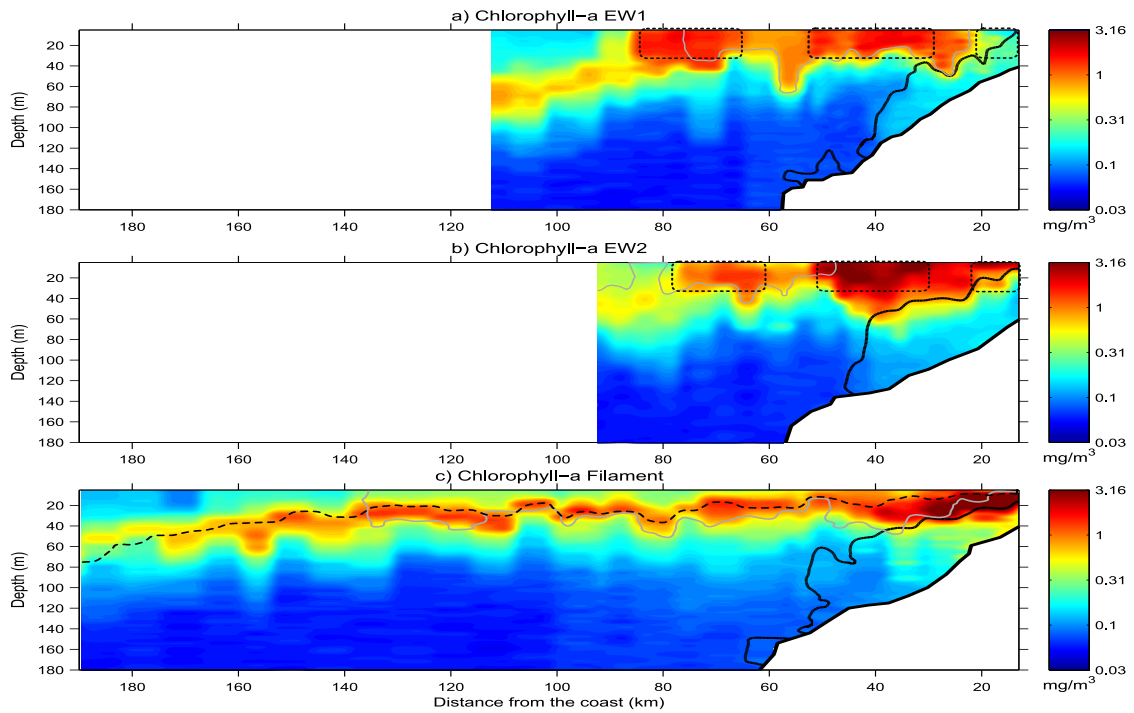


Figure 9: Distance from the coast (km) versus depth profiles of chlorophyll *a* concentrations (from fluorometer, converted in mg/m^3) along a) EW1 b) EW2 and c) EW within the filament. Black contours on the profile indicate the maximum of AOU concentrations ($> 60 \mu\text{mol}/\text{kg}$, corresponding roughly to dissolved oxygen concentrations $< 200 \mu\text{mol}/\text{kg}$). 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.

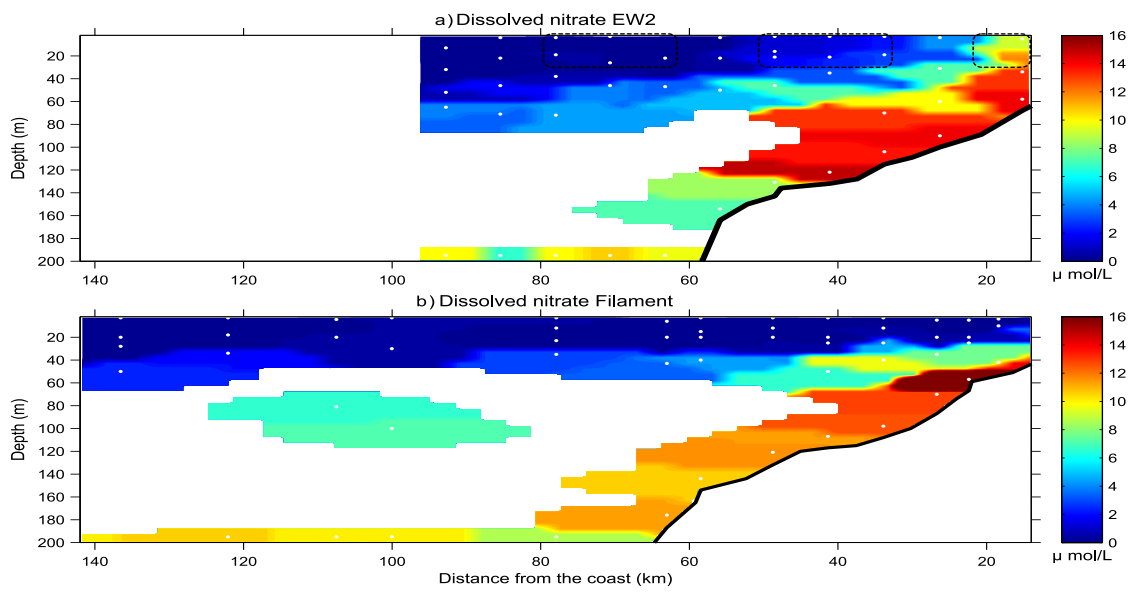


Figure 10: Distance from the coast (km) versus depth profiles of Nitrate concentrations (from water samples in $\mu\text{mol/l}$) along a) EW2 and b) EW within the filament. White markers indicate the measurement positions; white areas are regions where data were too sparse to be robustly interpolated.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

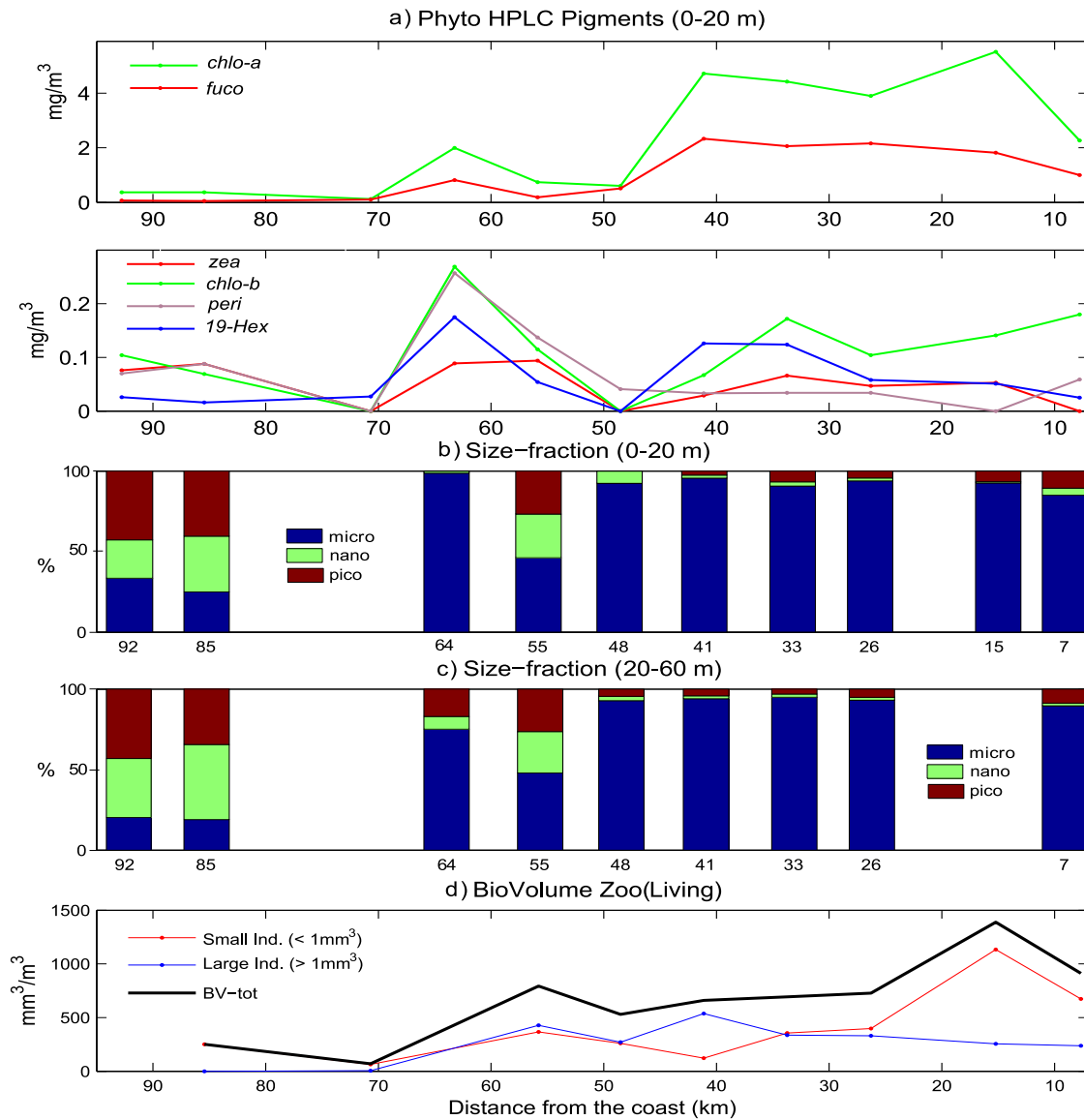


Figure 11: All data are for section EW2 at 40°N. a) Selected phytoplankton pigments surface concentrations from HPLC (0-20 m, two upper panels); b,c) size-fractionated phytoplankton composition (percentage) at the surface (0-20 m) and sub-surface (20-60 m); d) Zooplankton biovolume (size-fractionated)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

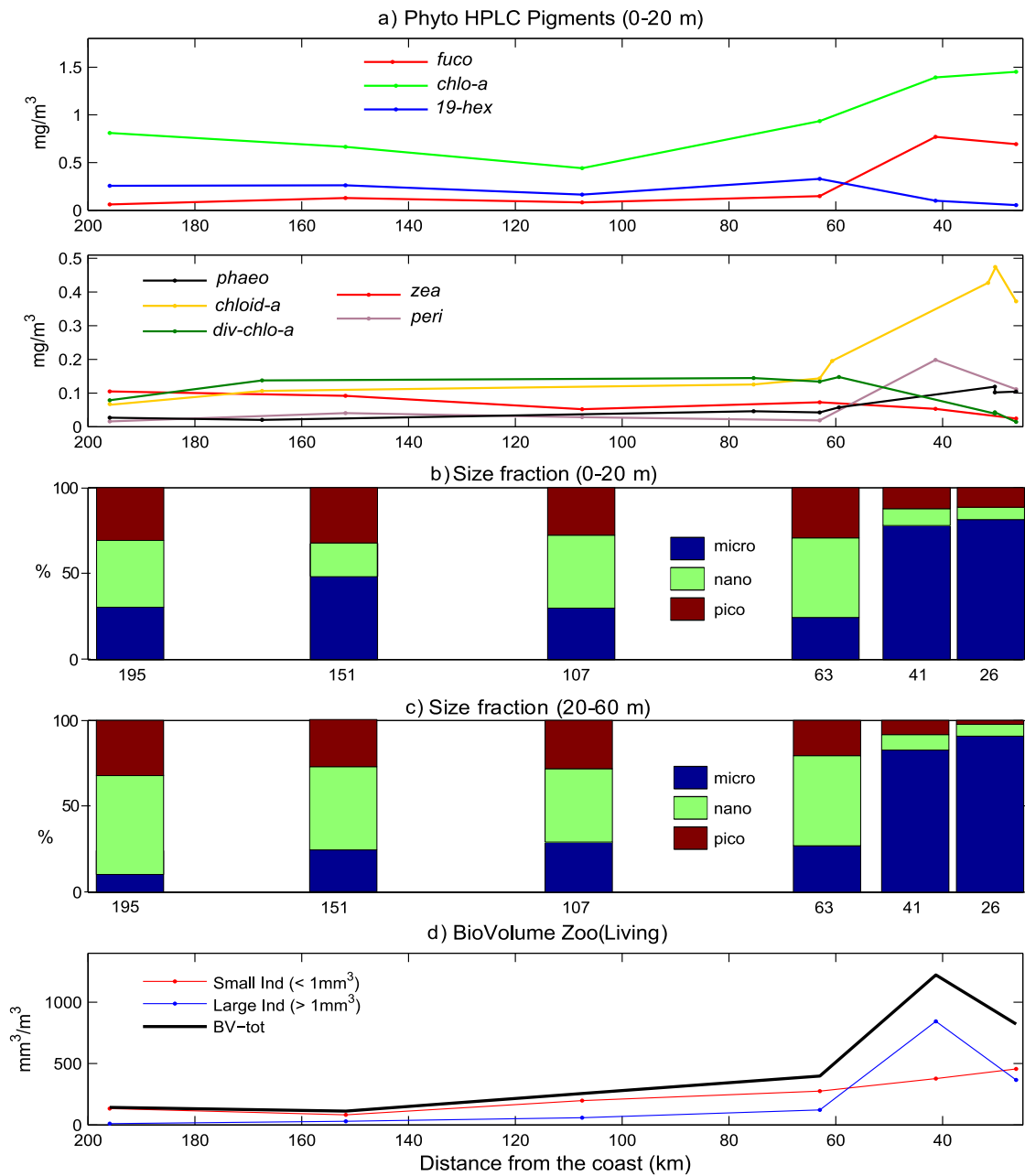


Figure 12: All data are for section EW within the filament. a) Selected phytoplankton pigments surface concentrations from HPLC (0-20 m, two upper panels); b,c) size-fractionated phytoplankton composition (percentage) at the surface (0-20 m) and sub-surface (20-60 m); d) Zooplankton biovolume (size-fractionated)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

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