

1 Dynamic of organic matter and meiofaunal community on a river-dominated shelf  
2 (Rhône prodelta, NW Mediterranean Sea): responses to river regime

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21 **Abstract:**

22 In the oligotrophic context of the Mediterranean Sea, riverine inputs of particulate organic matter  
23 represent an important source of food for benthic communities. However, since most of these inputs  
24 are delivered during short, but intense flood events, communities living in the vicinity of river mouths  
25 are also exposed to strong and frequent physical disturbances. A very tight and complex relationship  
26 links river dynamic and macrofaunal communities in Mediterranean deltas, but less is known on the  
27 response of meiobenthic communities to river regime. In 2010, sediments cores were collected in the  
28 Rhône River prodelta in winter and spring before the flooding of the Rhône River tributaries in June, and  
29 then twice in the early and late summer. The hypothesis was that increased runoff and export of  
30 terrigenous material would induce major changes in the sediment biochemistry, which would in turn  
31 trigger modifications in abundances and vertical distribution of the meiofauna. The origin and quality  
32 (lability, degradation state) of the different pools of organic matter preserved in these recent sediments  
33 were determined using bulk geochemical and molecular analyses (fatty acids, amino acids). Vertical  
34 profiles of descriptors for organic matter origin and quality revealed major changes in the nature of the  
35 inputs occurring at monthly time scales. Inputs of plant detritus from autumnal and winter flood events  
36 were still visible in the cores collected in February and April. A few days after the June 2010 high-  
37 discharge event, a newly deposit (~ 7 cm) containing soil organic matter has recovered the prodeltaic  
38 sediments and the resident meiofaunal community, but at the end of August only 2 cm of this deposit  
39 remained. Multivariate analyses furthermore highlighted that the meiofaunal community was driven by  
40 both the trophic conditions and deposition of a new sediment layer driven by the hydrological regime  
41 of the Rhône River. In April, increased abundances of meiofauna were observed in response to the  
42 sedimentation of labile organic matter after the spring bloom. The June high-discharge event affected  
43 the meiofauna with a reduction of its abundance and the burial of the resident meiobenthic community.  
44 However, the meiofauna recovered in less than two months after this disturbance, showing the strong  
45 resilience of this component of the benthic ecosystem in this high energy environment.

46 **Keywords:** Mediterranean Sea, Rhône River, high-discharge event, physical disturbance, marine  
47 sediments, organic matter, meiofauna

48 **1. Introduction**

49 Rivers represent the main source of fresh water, nutrients, sediments and terrestrial organic  
50 carbon (OC) to the coastal ocean. Continental shelves influenced by large to medium-sized rivers  
51 consequently account for some of the most biologically productive marine systems on Earth and have  
52 great ecological, biogeochemical, social and economic values (Day et al., 2019b). River flow dynamic,  
53 land use, coastal circulation, resuspension and meteorological events are all parameters that exert some  
54 level of control on the delivery and dispersal of riverine inputs of sediments and OC on the shelf. Human  
55 activities such as deforestation, agriculture, urbanisation, fluvial regulation and diversion affect the land-  
56 ocean export, both quantitatively and qualitatively (Bianchi and Allison, 2009). These transitional areas  
57 are also particularly vulnerable to climate-driven disturbances associated with global warming, sea-level  
58 rise and the increasing frequency and intensity of storms (O’Leary et al., 2017). How natural and  
59 anthropogenic changes in the delivery of terrestrial OC to continental shelves will affect global OC  
60 budgets remains largely uncertain (Bauer et al., 2013). Likewise, benthic communities play a central role  
61 in the cycling and burial of OC in estuarine ecosystems, but they are particularly exposed to combined  
62 anthropogenic stressors (Akoumianaki et al., 2013, 2006; Martin et al., 2019). Given this, the question  
63 is how and to what extent, changes in river inputs have an impact on benthic communities and the  
64 regulating services they provide.

65 Deltas are peculiar estuaries that form where sand and mud supply exceeds sediment dispersal.  
66 Their existence and functioning are therefore closely linked to river inputs (Giosan et al., 2014). A  
67 plethora of river delta systems have formed in the microtidal wave-influenced setting of the  
68 Mediterranean Sea (Besset et al., 2017). The watersheds and fluvial regime of most Mediterranean  
69 deltas, including the Ebro, Rhône, Po and Nile, have undergone severe modifications to accommodate  
70 human activities (Day et al., 2019a). Despite considerable efforts to control the runoff of these rivers,  
71 the export of particulate matter takes place primarily during high discharge flood events triggered by  
72 intense rainfalls or oceanic storms (Antonelli et al., 2008). Depending on the season and drainage basin  
73 affected, the magnitude and nature of the particulate organic matter (POM) exported during these

74 events are highly variable with inputs of fossil OC, eroded soils, riparian vegetation or phytoplankton  
75 (Antonelli et al., 2008; Cathalot et al., 2013; Harmelin-Vivien et al., 2010; Higuera et al., 2014; Marion  
76 et al., 2010; Tesi et al., 2008). Meteorological and hydrological drivers are thus expected to control the  
77 supply and quality of the POM delivered to the shelf as well as its bioavailability for the benthic fauna.  
78 Moreover, extreme flooding events results in the rapid deposition of fine terrigenous particles which  
79 have significant effects on the structure and function of macrobenthic communities (Cardoso et al.,  
80 2008; Lohrer et al., 2004; Norkko et al., 2002). For instance, off the Rhône River, the proliferation of  
81 opportunist species taking advantage of flood deposits has been observed in the months following  
82 major events (Salen-Picard et al., 2003). A very tight and complex relationship links river dynamic and  
83 macrofaunal communities in Mediterranean deltas (Akoumianaki and Nicolaidou, 2007; Bonifácio et al.,  
84 2014; Hermand et al., 2008; Salen-Picard et al., 2003). By contrast, meiobenthic communities (animals  
85 retained between 40 µm and 1 mm mesh size of sieves; Giere, 2009) from deltaic systems have received  
86 little attention (Danovaro et al., 2000; Guidi-Guilvard and Buscail, 1995; Palacín et al., 1992, Semprucci  
87 et al., 2019) at the notable exception of foraminiferans (Fontanier et al., 2008; Franzo et al., 2019;  
88 Goineau et al., 2012). The meiofauna has an important role in the functioning of benthic ecosystem,  
89 contributes significantly to the diet of many other animals (Coull, 1990), and facilitates mineralisation  
90 of organic material (Coull, 1999; Gee, 1989; Riera and Hubas, 2003). Because of their small size, lack of  
91 larval stage and shorter generation time, meiobenthic organisms respond more successfully than the  
92 macrofauna to changes in environmental conditions (Balsamo et al., 2012). As such, meiofaunal  
93 communities have been widely used to monitor the effects of both natural and anthropogenic  
94 perturbations in aquatic ecosystems (Coull and Chandler, 1992; Gambi et al., 2003; Schratzberger and  
95 Ingels, 2018, Semprucci et al., 2018). Although the meiofauna appears as a good bioindicator of organic  
96 enrichment and physical disturbance in coastal areas (Gambi et al., 2003), there is a paucity of studies  
97 focusing on their response to river inputs (Danovaro et al., 2000; Guidi-Guilvard and Buscail, 1995;  
98 Palacín et al., 1992; Pelletier et al., 1999).

99            In this study, the response of meiofaunal communities to the dynamic of river inputs is  
100 discussed. In 2010, we had the opportunity to study the impact of a high-discharge event of the Rhône  
101 River, the largest Mediterranean river. Sediments were collected in the winter and spring before this  
102 period and afterwards, twice in the early and late summer. The hypothesis was that this extreme event  
103 would induce major changes in the sediment biochemistry, which would in turn trigger modifications in  
104 abundances and vertical distribution of the meiofauna. The specific aims of the present study were (1)  
105 to evaluate how the Rhône River regime affect sediment biochemistry in the prodelta at a seasonal time  
106 scale, (2) to investigate whether the main taxa of the meiofauna respond to changes in river inputs, and  
107 (3) to determine which of the investigated environmental parameters (i.e. grain-size, porosity,  
108 sedimentary organic matter composition, stable isotopic values...) were the most pertinent to illustrate  
109 the observed trends. A particular attention was paid at determining the origins and quality of the POM  
110 delivered by the Rhône River, as it represents fresh sources of detritus for benthic organisms.

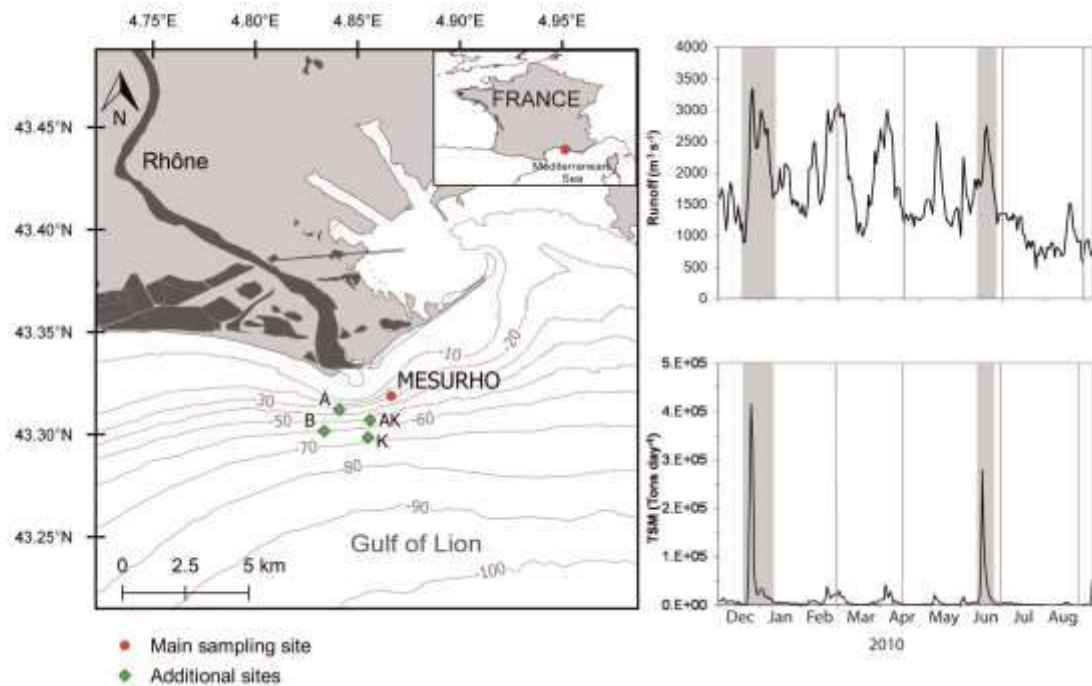
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## 112 2. Materials and methods

### 113 2.1. Regional setting and study area

114            The Rhône River, now the main river in the Mediterranean Sea since the damming of the Nile,  
115 links the Rhône glacier in the Swiss upper Alps to the Camargue delta on the French coast of the  
116 Mediterranean Sea (the Gulf of Lion). It is mainly an Alpine river, which drains a relatively small (95,000  
117 km<sup>2</sup>), but highly diversified, watershed exhibiting a strong geological heterogeneity (Olivier et al., 2009).  
118 The Rhône catchment includes several climatic zones (mountainous, oceanic and Mediterranean)  
119 resulting in a very complex hydrological regime and a strong inter annual variability (Pont et al., 2002).  
120 Typical of Mediterranean rivers, the runoff of the Rhône is characterised by flooding events triggered  
121 by intense rainfalls in autumn and snowmelt in spring. As a consequence, solid export to the Gulf of Lion  
122 occurs mainly during short, but intense high-discharge events (Antonelli et al., 2008). Riverine  
123 particulate inputs undergo a rapid deposition near the river mouth in the prograding prodelta (Maillet  
124 et al., 2006). The unconsolidated sediments are frequently resuspended by episodes of strong winds or

125 by near bottom currents (Ulses et al., 2008). The study area is located at 2.5 km of the Rhône River  
126 mouth in the prodelta area (Fig. 1).



127  
128 **Figure 1: Location of the sampling sites in the Gulf of Lion (left) and Rhône River runoff and total**  
129 **suspended matter (TSM) concentration for 2010 (right).** Rhône data were measured at the SORA  
130 Observatory Station in Arles, the most downstream gauge station, 40 km upstream the mouth. The  
131 vertical bars indicate the sampling dates and the grey areas represent periods of high solid discharge  
132 rate.

## 133 134 2.2. Hydrological and climatic conditions

135 Mean daily discharge data from the Arles gauging station were provided by the CNR (Compagnie  
136 Nationale du Rhône, the main hydropower company on the Rhône River). Daily total suspended matter  
137 (TSM) concentrations measured in water samples collected at the Rhône observatory station at Arles  
138 (SORA) were provided by the MOOSE network (Mediterranean Oceanic Observing System for the  
139 Environment – <http://www.moose-network.fr>). Monthly weather reports were provided by Météo  
140 France.

141  
142

### 143 2.3. Sediment sampling

144 The sampling targeted four contrasted periods in 2010: winter (20<sup>th</sup> February), spring (18<sup>th</sup>  
145 April), early (1<sup>st</sup> July) and late summer (28<sup>th</sup> August). Sediment cores were collected at station MESURHO  
146 (43°19.2 N, 4°52 E, 20 m depth) from the board of the Téthys II R/V using a multicorer MUC 8/100  
147 (Oktopus GmbH) during the field campaigns MESURHOBENT 1, 2, 3 and 4 (Rabouille, 2010a, b, c, d). At  
148 each sampling date, four undisturbed sediment cores (9.5 cm of diameter and 60 cm of height) were  
149 processed on board and sliced into seven horizontal layers (0–0.5, 0.5–1, 1–2, 2–3, 3–5, 5–7 and 7–10  
150 cm). Since previous studies in the prodelta area have shown that variability among cores was low  
151 (Bourgeois et al., 2011; Cathalot et al., 2010; Pastor et al., 2011a), one core was conditioned in this study  
152 for sediment characterisation. Sediment layers were carefully homogenised, distributed in two aliquots  
153 and immediately frozen at -20°C. Sediment layers from the three other cores were preserved in 70%  
154 alcohol for meiofaunal analysis. Visual observation of the sediment cores used in this study showed no  
155 signs of burrows, biogenic structures, oxic voids or large macrofauna, suggesting low bioturbation  
156 activity.

157

### 158 2.4. Assessment of sediment characteristics

159 Sediment granulometry was assessed using a Malvern® Mastersizer 2000 laser diffraction  
160 particle size analyser. Porosity ( $\phi$ ) was calculated by determining water mass loss during drying  
161 assuming a value of 2.63 g.cm<sup>-3</sup> for grain size density and 1.03 g.cm<sup>-3</sup> for pore water density. Sediment  
162 granulometry, and porosity were determined in triplicate for each sample.

163 Elemental and biochemical analyses were performed on freeze-dried sediments. The analytic  
164 protocols for total organic carbon (TOC), bulk stable carbon isotopes ( $\delta^{13}\text{C}$ ), total hydrolysable amino  
165 acids (THAA) and fatty acids have been described in Fagervold et al. (2014).

166 Enzymatically hydrolysable amino acids (EHAA), which correspond to the fraction of amino acids  
167 assumed to be bioavailable for benthic deposit-feeders, were extracted by the biomimetic approach of  
168 Mayer et al. (1995). THAAs and EHAAs were analysed by reverse phase high-performance liquid



169 chromatography (HPLC, Gynkotek-Dionex system) following precolumn derivatisation with  
170 orthophthaldialdehyde (Lindroth and Mopper, 1979). The isoindol derivatives were separated on a C18-  
171 HPLC column using a non-linear gradient of methanol-acetate buffer and were detected by fluorescence  
172 at 450 nm using an excitation wavelength of 335 nm (Bourgeois et al., 2011).

173 Fatty acid, THAA and EHAA concentrations were normalised to total organic carbon.

174

## 175 2.5. Assessment of meiofaunal abundance and taxonomic composition

176 The sediment samples were sieved through 1000 and 40 µm mesh simultaneously. The fraction  
177 retained on the 40 µm sieve was collected and centrifuged with Ludox HS 40 (density 1.15) as described  
178 by Heip et al. (1985). The organisms in the supernatant were collected and rinsed on a 40 µm mesh to  
179 remove Ludox and preserved in 70% alcohol. All meiobenthic organisms were counted and classified to  
180 higher taxon under a stereomicroscope, after staining with rose Bengal. A sample splitter, Motoda-box  
181 (Motoda, 1959) was used to obtain an aliquot containing about 1000 organisms, for the abundance  
182 estimations of nematodes and copepods. The number of other meiobenthic taxa was too low to  
183 evaluate on split samples, they were thus counted on the whole sample. Total density of meiofauna and  
184 of the main representative taxa (nematodes, copepods, annelids, cumaceans, turbellarians,  
185 foraminiferans, and kinorhynchs) were determined (number of individuals/10 cm<sup>2</sup>) for the four sampling  
186 dates. Mean density based on the 3 cores were calculated for each layer. Note that the Ludox extraction  
187 is less efficient for organisms with shells, like foraminiferans, molluscs or ostracods, and that the  
188 abundances were thus underestimated for these taxa.

189

## 190 2.6. In situ microprofiling of dissolved oxygen and DOU calculation

191 A benthic lander carrying a benthic microprofiler (Unisense®) was deployed to measure *in situ*  
192 microprofiles of dissolved oxygen (Cai and Reimers, 1993; Rabouille et al., 2003; Rassmann et al., 2020  
193 and references therein). The benthic lander was deployed in April, July and August 2010 at a maximum  
194 of 5 stations, except in August because of bad weather conditions. These stations encompass the

195 MESURHO station, another proximal station located in the South of the Rhône River (A), and 3 other  
196 stations located in the Rhône prodelta (AK, B and K, Fig. 1).

197 Four oxygen microelectrodes were simultaneously deployed, and vertical depth profiles were  
198 measured with a 200 µm resolution together with a resistivity electrode. As their response to variations  
199 in oxygen concentrations is linear (Boudreau and Jorgensen, 2001), the O<sub>2</sub> microelectrodes were  
200 calibrated with a two-point calibration technique using the bottom water O<sub>2</sub> concentration determined  
201 by Winkler titration and the anoxic pore waters. Signal drift of O<sub>2</sub> microelectrodes during profiling was  
202 checked to be less than 5 %. Diffusive oxygen uptake (DOU) rates were calculated using Fick's first law  
203 (Berner, 1980, Eq. 3),

$$204 \quad DOU = -\phi \cdot D_s \cdot \left. \frac{d[O_2]}{dz} \right|_{z=0} \quad (3)$$

205 where  $\phi$  is sediment porosity,  $D_s$  the diffusion coefficient in the sediments (cm<sup>2</sup> s<sup>-1</sup>), and  
206  $\left. \frac{d[O_2]}{dz} \right|_{z=0}$  is the oxygen gradient below the sediment water interface (µmol cm<sup>-4</sup>). For the calculations,  
207 the gradient between 0 and 400 µm in the sediment was consistently used. The  $D_s$  coefficients were  
208 adjusted for diffusion in a porous environment according to:  $D_s = \frac{D_0}{(1+3 \cdot (1-\phi))}$  with the diffusion  
209 coefficient in free water ( $D_0$ ) taken from Broecker and Peng (1974) and recalculated at *in situ*  
210 temperature using Li and Gregory (1974).

211

## 212 2.7. Data analysis

213 The amount, sources, and quality of the sedimentary organic matter (OM) in the Rhône prodelta  
214 were assessed with a suite of bulk and molecular descriptors. The list of the parameters used in this  
215 study is provided in Table 1 with their interpretation. The degradation index (DI) was calculated from  
216 the molar composition of the THAA hydrolysates (Dauwe et al., 1999a). This index synthesises subtle  
217 changes in the amino acid composition linked with diagenesis into a univariate variable indicative of OM  
218 degradation stage, whose value decreases with increasing degradation. We applied the same calculation  
219 on the EHAA composition of the flood deposit. In this case, the index (DI<sub>EHAA</sub>) provided information on

220 the degradation stage of the pool of amino acids that may be assimilated by benthic organisms. The  
221 reactivity index  $[RI=(\text{tyrosine}+\text{phenylalanine})/(\beta\text{-alanine}+\gamma\text{butyric acid})]$  is another indicator of OM  
222 degradation (Jennerjahn and Ittekkot, 1997). It takes into account two opposite trends: the reactive  
223 aromatic amino acids, tyrosine and phenylalanine, are rapidly degraded in decaying OM, whereas their  
224 decarboxylation products,  $\beta$ -alanine and  $\gamma$ -butyric acid, consistently increase with microbial degradation  
225 (Alkhatib et al., 2012; Jennerjahn and Ittekkot, 1997).

226 A one-way ANOVA was used to analyse variations in total meiofaunal abundance whereas two-  
227 ways ANOVA were performed to test for differences in meiofaunal vertical distribution with time, with  
228 sediment depth and time x sediment depth. Abundances were double square root transformed in order  
229 to meet the assumptions for ANOVA (homogeneity of variances, normally distributed residuals). A Tukey  
230 Honest Significance Test (HSD) test was applied when significant differences were detected between  
231 means. Analyses of variance were run with XLSTAT (V4.01).

232 A principal component analysis (PCA) was then performed to reveal trends in OM composition  
233 that could help us retrace the recent history of riverine particle inputs in the prodelta. Prior to PCA, a  
234 correlation analysis of the environmental variables was performed to identify variables that were highly  
235 correlated, retaining only one of these variables. PCA was combined to hierarchical clustering of the  
236 PCA components (HCPC), which determines clusters of samples that present homogenous  
237 characteristics (Husson et al., 2010). The HCPC was performed on the 5 first components of the PCA  
238 (accounting for 91% of the total variance) using Ward's agglomerative method and a Euclidean distance.  
239 PCA and HCPC were performed using R software (3.4.4) with the package 'Rcmdr – Factominer' (Lê et  
240 al., 2008).

241 Relationships between the abundance of meiofaunal taxa and factors, representing sediment  
242 characteristics, were summarised using a Canonical Correspondence Analysis (CCA) (ter Braak, 1986)  
243 performed with the R package 'vegan' (Oksanen et al., 2016). CCA allowed to simultaneously visualise  
244 the abundances of the principal meiofaunal taxa, the optimal niches (sample corresponding to sediment  
245 depth x date) with the environmental parameters (Borcard et al., 2011). The environmental variables

246 identified by PCA were first retained. The “vif.cca” function of ‘vegan’ was then used to identify  
247 redundant constraints (i.e. environmental variables with variance inflation factors >10) and were  
248 removed from the analysis to reduce collinearity. CCA was finally performed on square root transformed  
249 abundances to reduce the weight of abundant taxa and a subset of standardised environmental  
250 variables describing the quality of food available for the meiofauna ( $\delta^{13}\text{C}$ , C/N ratio, normalised  
251 concentration in EHAA, EHAA/THAA ratio, DI, % Algal PUFA) or related to sediment properties (porosity,  
252 % clay, and  $\text{CaCO}_3$ ). The statistical significance of the overall relationship and of the canonical axes were  
253 evaluated using Monte Carlo permutation tests (999 permutations). The CCA ordination diagram  
254 displayed samples and taxa as points and environmental variables as vectors (Borcard et al., 2011).  
255 Finally, the relative importance of the explanatory variables was evaluated by forward selection  
256 followed by Monte Carlo permutation tests (999 permutations) using the “ordistep” function of ‘vegan’  
257 (Blanchet et al., 2008). With this method, all variables are ranked on the basis of their marginal effects  
258 (i.e. considering each variable as the sole constraining variable) and conditional effects (i.e. forward  
259 selection on the best descriptors and evaluation of the fit of each variable in conjunction with the  
260 variable(s) already selected).

261 Result outputs for ANOVA and multivariate analyses are provided in the supplementary  
262 material.

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### 264 3. Results and discussion

#### 265 3.1. Hydrological and climatological conditions

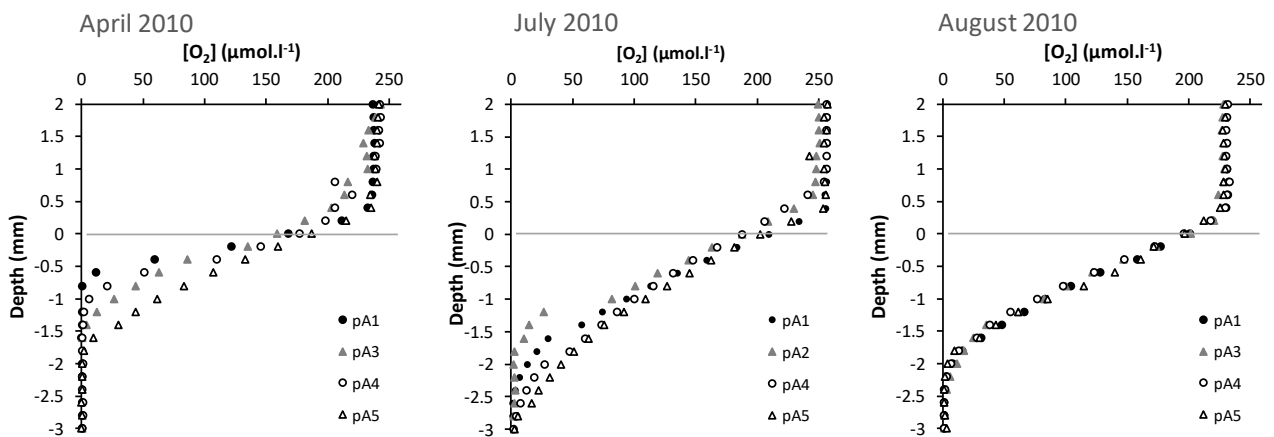
266 In 2010, the French Mediterranean coast experienced a cold and rainy winter with strong winds  
267 dominated by Mistral. Rains were frequent, but moderate with Rhône water discharge reaching  $2500\text{m}^3$   
268  $\text{s}^{-1}$  ten days before February sampling and  $3000\text{m}^3 \text{s}^{-1}$  on the sampling date (Fig. 1). The organic content  
269 of the total suspended matter (TSM) was high (TOC= 7.81% on the 12<sup>th</sup> of February 2010, Kerhervé  
270 unpublished result). March was also rainy and windy. Two minor floods occurred before the April  
271 sampling, but TSM only slightly increased during these events. In April, the weather was fair with little

272 wind and precipitation, but liquid discharge rates were high, possibly because of snow melting. As a  
273 consequence, TSM increased above  $100\text{mg.L}^{-1}$ . On the 15<sup>th</sup> and 16<sup>th</sup> of June 2010, exceptional stormy  
274 rains (40cm per day) have generated severe flooding in south-eastern France. This rare and deadly flash  
275 flood event is believed to be the most important since 1827 (Payrastre et al., 2012). Rainfalls mostly  
276 affected the southeast tributaries of the Rhône River (the Durance, the Buëch, the Verdon, etc.) causing  
277 their overflow. The runoff of the Rhône River peaked at  $2600\text{m}^3.\text{s}^{-1}$ , while solid discharge reached  $2.8$   
278  $10^5$  tones on June 16, 2010. In the days before return to normal runoff, the Rhône brought  
279 approximately one fourth of the annual solid input for 2010. The summer was dry and hot. The daily  
280 runoff rate was below the mean inter annual flow rate of  $1700\text{ m}^3\text{s}^{-1}$  and was typical of low river flow  
281 ( $500\text{-}1000\text{ m}^3\text{s}^{-1}$ ). July was characterised by strong winds generally oriented N-NW (12 to 13 days of  
282 Mistral). The wind changed of direction on the 26<sup>th</sup> of July (S) and generated a storm regime.  
283 Meteorological conditions were similar on August with episodes of strong winds.

284

### 285 3.2 Oxygen penetration depth and metabolic activity traced by diffusive oxygen uptake (DOU) in the 286 Rhône prodelta

287 The oxygen microprofiles recorded *in situ* at station MESURHO display a large decrease below  
288 the sediment-water interface over depth of a few millimetres, below which the sediment was  
289 completely anoxic (Fig. 2). A clear change in time for the oxygen penetration depth (OPD) is visible on  
290 figure 2 with average values of  $1.4 \pm 0.5$  mm in April 2010,  $2.6 \pm 0.5$  mm in July 2010, and  $2.4 \pm 0.2$  mm  
291 in August 2010.



292 Figure 2: Dissolved oxygen microprofiles at the sediment-water interface recorded *in situ* at the MESURHO  
 293 station in April, July, and August 2010. Each symbol represents a single electrode profile. The line at 0  
 294 mm indicates the sediment surface.

295

296 This increase in OPD is accompanied by a decrease of DOU (Table 2), which is a proxy of the metabolic  
 297 activity in the sediments based on organic matter mineralisation (Cathalot et al., 2010; Rassmann et al.,  
 298 2020). The DOU recorded at 5 stations in the prodelta show a decrease from April to July, with a levelling  
 299 in August for the only record that we have at the MESURHO station. The decrease of DOU at the spring-  
 300 summer transition in 2010 contrasts with the normal spring-summer situation with fresh organic matter  
 301 deposition and bottom water warming, which generates more mineralisation in surface sediments  
 302 (Lansard et al., 2008). This unusual decrease in early summer could be related to the high-discharge  
 303 event in June and the deposition on the seabed of low reactivity material as happened in 2008 during a  
 304 flood carrying significant amount of material from the Durance tributary (Cathalot et al., 2010). The  
 305 decrease was more pronounced for stations MESURHO and AK (~ 40% decrease), which are directly  
 306 under the influence of the Rhône River inputs, and more limited for stations B and K, suggesting lower  
 307 disturbance with increasing distance from the river mouth.

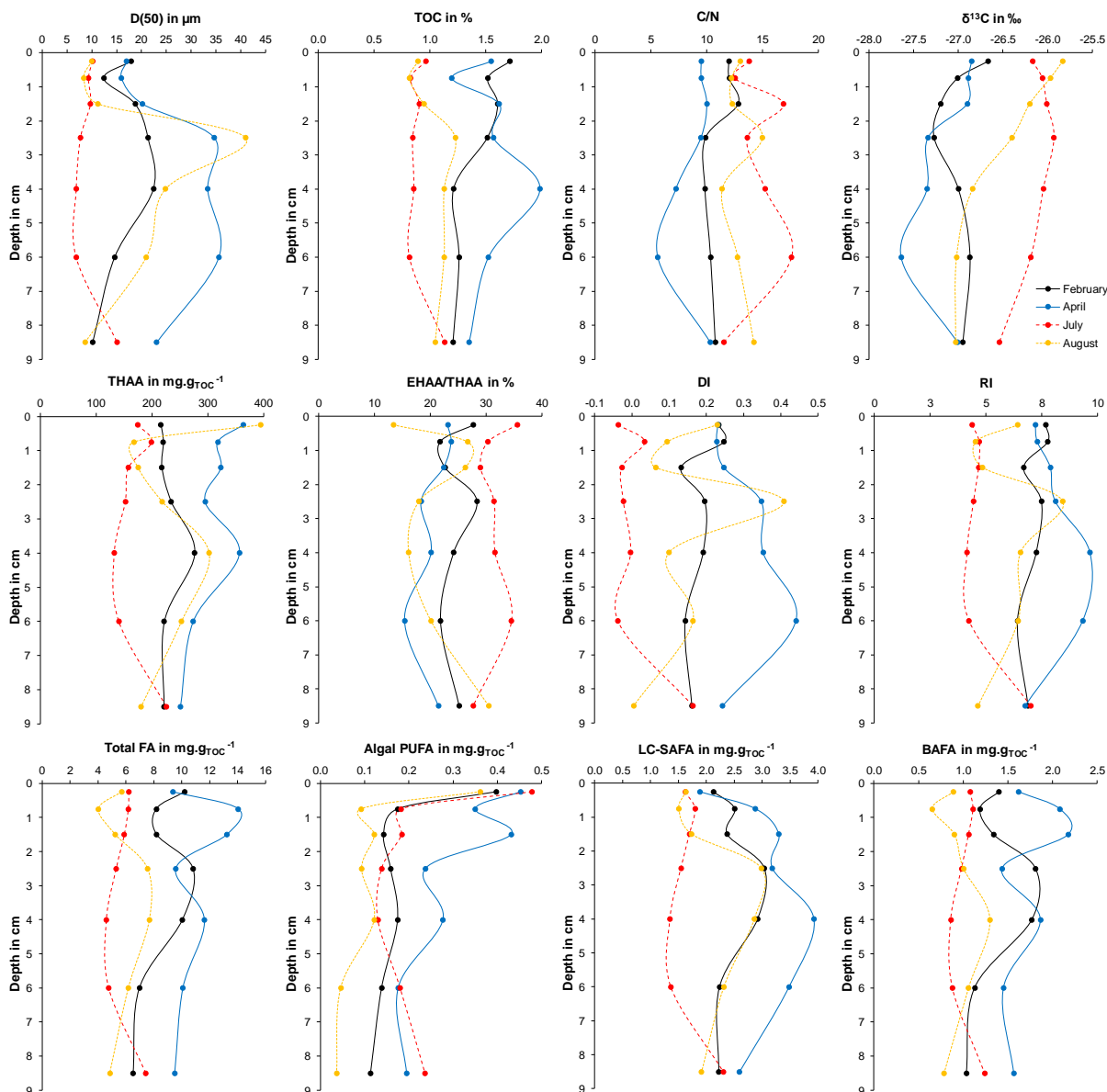
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### 310 3.3. Short-term chronicle of particulate organic matter inputs in the Rhône prodelta

311 Short sediment cores collected in deltaic areas are useful records of the recent history of  
312 riverine POM inputs in coastal areas (Cathalot et al., 2010; Leithold and Hope, 1999). The down-core  
313 evolution of sedimentary OM composition provides insights on temporal changes in the characteristics  
314 of the POM available for the benthic fauna (Goineau et al., 2012). Clearly, the down-core profiles of  
315 organic compounds are far from a textbook situation with steady inputs of OM from the overlying water  
316 and progressive degradation on the seafloor (see for instance TOC profiles, Fig. 3). Likewise, descriptors  
317 of OM origin ( $\delta^{13}\text{C}$ , fatty acid subgroups) and quality (C/N, EHAA/THAA, DI, RI) point to major changes in  
318 the nature of the inputs occurring at a monthly time scale (Fig. 3).

319 In February, sampling occurred early at the very onset of a Rhône River flood. High organic  
320 contents were observed through the sedimentary column, with an integrated TOC content of 1.4% for  
321 the ten first centimetres of sediment (Fig. 3). The normalised concentrations in THAA and fatty acids  
322 were also high. Descriptors of OM quality and origins revealed strong differences between the surface  
323 sediment and the layers below. Phytoplankton markers were only found in the upper layer indicating  
324 either the rapid degradation of this labile fraction within the sediments or a recent pulse of POM  
325 deriving from microalgae. This assumption is further supported by an enriched  $\delta^{13}\text{C}$  value as well as by  
326 descriptors of OM quality (DI, RI, and EHAA/THAA ratio), which exhibited slightly higher values on the  
327 surface than in the layers below (Fig. 3). Subsurface and deeper layers were enriched in coarse material  
328 and markers of plant detritus (long chain fatty acids) and had a constant C/N ratio of  $\sim 10$ . These  
329 biomarkers associated to high TOC contents and a coarser material are consistent with the preservation  
330 of plant detritus brought in autumn and winter.



332 **Figure 3: Down-core evolutions of sediment properties at the MESURHO station in February, April, July,**  
 333 **and August 2010.** D(50)= median grain size, TOC= total organic carbon, C/N= molecular carbon to  
 334 nitrogen ratio,  $\delta^{13}\text{C}$  = bulk stable isotope value, THAA= normalised total hydrolysable amino acid  
 335 concentration, EHAA/THAA= proportion of enzymatically hydrolysable amino acids, DI= degradation  
 336 index value, RI= reactivity index, Total FA, Algal PUFA, LC-SAFA and BAFA= TOC-normalised  
 337 concentrations in total fatty acids, algal polyunsaturated fatty acids, long chain saturated fatty acids and  
 338 bacterial fatty acids.

339

340 In April, sedimentary characteristics were more heterogeneous on the 10cm layer than during  
 341 the winter (Fig. 3). TOC content was still high and comparable to February in the surface sediment, but



342 at 3-7cm depth, a layer enriched in markers of plant detritus was observed. At the surface, high  
343 concentrations in planktonic markers were again suggestive of phytoplankton inputs. Organic carbon,  
344 amino acids and fatty acids tended to be higher in the subsurface sediments. This coarser subsurface  
345 layer was also less degraded (higher DI and RI) with a lower bioavailability of the amino acid pool.  
346 Globally, this suite of descriptors indicates that plant detritus have been exported during the two floods  
347 that preceded the sampling, or that earlier deposits in the mud belt have been remobilised. Porosity  
348 was also discontinuous, in agreement with the successive deposition of different layers of material.

349           The grain size distribution shows the deposition of about 7 cm of fine particles on the sediment  
350 after the torrential rainfalls in June (Fig. 3, 96% of particles <63 $\mu$ m). The sudden peak of TSM (Fig. 1)  
351 certainly accounted for this deposit, which was depleted in organic carbon and nitrogen. The flood  
352 deposit was also depleted in labile components such as fatty acids and hydrolysable amino acids (on  
353 average only ~7% of the TOC was found in the THAA) and was globally more degraded (lower DI and RI)  
354 than the material delivered during periods of normal discharge. The characteristics of this fine material  
355 recall the one delivered by the Rhône River during the flood of the Durance tributary in June 2008  
356 (Bonifácio et al., 2014; Pastor et al., 2018). Following this event, a flood deposit of ~30 cm was observed  
357 in the prodelta area (Cathalot et al., 2010). This organic-poor material had a peculiar  $\delta^{13}\text{C}$  signature (-  
358 25.8‰) and displayed a  $\Delta^{14}\text{C}$  of -495‰ in relation with the refractory nature of the eroded watershed  
359 and the flushing of the Serre-Ponçon dam on the Durance (Cathalot et al., 2013; Copard et al., 2018).  
360 The decrease in remineralisation activity in the surface sediments after these two events is a further  
361 indication that the deposited material was poorly reactive (Table 2).

362           The trend for lower porosities at the end of August suggests that the summer conditions allowed  
363 the muddy deposits to settle and become more compact (Table S1, supplementary material). This is  
364 consistent with the concomitant stratification of the microbial community described by Fagervold et al.  
365 (2014) at this station. Organic content was still low, but OM characteristics indicate intense reworking  
366 of the sediments since July (Fig. 3).  $\delta^{13}\text{C}$  values ranged from “flood signature” of the tributaries (~ -26‰)  
367 in surface to the usual winter value of the Rhône (~ -27‰). Below the first two centimetres, which kept

368 the flood imprint, the sediment was enriched in TOC, amino acids, fatty acids, and long chain fatty acids.  
369 The down-core evolution of the DI is difficult to interpret. In the surface layer (0-0.5cm), the DI value  
370 was similar to values found in February and April on the top of the cores and may be indicative of the  
371 recent export of TSM by the Rhône River. Values for the 0.5-1 and 1-2cm layers were closed to those  
372 found in the flood deposit, between 2-3cm depth DI was similar to values measured in the April layer  
373 enriched with macrodetritus, and below DI was lower indicative of a more degraded pool of POM. Grain  
374 size followed the same trend as DI in good consistency with the hypothesis that the 2-3cm layer  
375 corresponded to sediments enriched in coarse macrodetritus. The proportion of bioavailable amino  
376 acids (EHAA/THAA) was also extremely variable along the sediment depth consistent with inputs of  
377 different sources of POM and non-steady state conditions.

378           Taken together all these results show that the flood deposit formed a thinner layer at the end  
379 of the summer in comparison to what settled in June. Estimation of the thickness of this layer is about  
380 1.5 to 2 cm depending on the parameters used. Compaction cannot entirely account for the reduction  
381 of the thickness of the flood deposit. Erosion is the most likely explanation. Strong winds occurred in  
382 July (26<sup>th</sup>) causing the resuspension of sediments at the MESURHO buoy (Lorthiois, 2012). The author  
383 described the sediment dynamic during this event as the resuspension of the non-consolidated  
384 sediments and their near bottom transport offshore. Dufois et al. (2014) have demonstrated that  
385 bottom erosion could be an important process for the sediment dynamic in the prodelta area during  
386 moderate river discharge and energetic events. Above the remaining flood deposit, some inputs of fresh  
387 suspended particulate matter (DI= 0.23) enriched in labile biogenic compounds (amino acids and fatty  
388 acids) have settled during the summer (Fig. 3). Underneath the flood deposit, older consolidated  
389 deposits from the autumn, winter and/or spring were found.

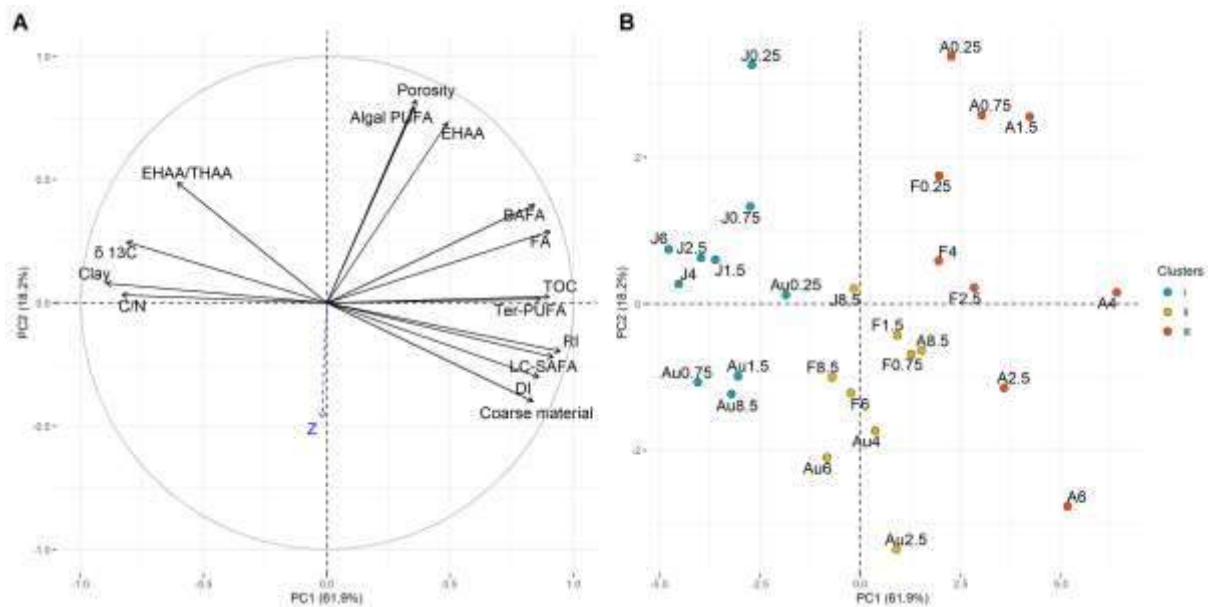
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392

393 **3.4. Sources and lability of the sedimentary organic matter in the Rhône prodelta**

394 Down-core evolutions of bulk and molecular descriptors of sedimentary organics in the prodelta  
395 highlight the occurrence of several pools of OM, whose dynamic of delivery is related to season and  
396 river regime. A PCA was performed to define the biochemical properties of these different pools of OM  
397 (Fig. 4).



398  
399 **Figure 4: Principal component analysis (PCA) of sediments collected in the Rhône River prodelta: loading**  
400 **plot (A) and score plot (B) for the first and second principal components (7 sediment layers × 4 dates).**  
401 Black arrows indicate active variables and the blue arrow corresponds to the supplementary variable  
402 (sediment depth: Z). Samples were clustered in 3 groups according to a hierarchical clustering analysis  
403 performed on the 5 first principal components of the PCA. Sample code is as follow: the letter indicates  
404 the month (F= February, A= April, J= July, Au= August) and the number corresponds to the mid-depth  
405 of the sediment layer (in cm). Clay= % of particles <4µm, Coarse material= % of particles >200µm, CaCO<sub>3</sub>  
406 = % of calcium carbonate. For all other variables see Table 1 for abbreviations. Concentrations in EHAAs,  
407 fatty acids (FA), BAFA, LC-SAFA, Terrestrial PUFA & Algal PUFA were normalised to organic carbon  
408 content.

410 Results of the PCA show that sediment properties can be summarised in two independent  
411 principal components explaining 80% of the total variance (Fig. 4A). Sediment layers were not grouped  
412 by dates or strata on the two first components of the PCA (Fig. 4B), which is consistent with the

413 successive deposition of particles originating from different sources. Two pools of organic inputs were  
414 clearly separated on the first component axis (PC1= 61.9 % of the total variance). A group of variables  
415 with positive loadings on PC1 characterised a coarser material enriched in TOC, fatty acids, and markers  
416 of vascular plants (LC-SAFA and Ter PUFA). This material also exhibited higher DI and RI values, indicative  
417 of limited diagenetic alteration, and depleted  $\delta^{13}\text{C}$  values consistent with an input of modern plant  
418 detritus in C3 ( $\delta^{13}\text{C}$  plant = -28‰, Hedges et al., 1986). Taken together, these results confirm that  
419 sediment cores collected in February and April 2010 were enriched in plant detritus (Fig. 4B, cluster II).  
420 A distinct source of OM associated to clay, low TOC content, higher C/N ratios and  $\delta^{13}\text{C}$  values was found  
421 in June and some sediment layers in August 2010 (negative loadings on PC1 and cluster I). OM in the  
422 flood deposit (Cluster I) was also more bioavailable for the benthic fauna as seen by higher EHAA/THAA  
423 ratios (Fig. 3). The second principal component (PC2= 18.2% of the total variance) illustrates variations  
424 that can be attributed to sediment depth, such as the decrease in porosity in the sedimentary column  
425 and the rapid degradation of the most labile components (PUFA deriving from phytoplankton and  
426 EHAA). The distribution of layers from the April core along PC2 agrees with this general pattern: the 2  
427 first centimetres (with positive loadings) being enriched in bioavailable OM, whereas the layers below  
428 (with negative loadings) contained a more refractory pool of OM. A second group of samples  
429 characterised by lower algal contents and porosity was also linked to PC2. This cluster regroups  
430 intermediate layers from August and some layers from February (cluster II on Fig. 4B).

431 The different molecular descriptors used in this study enable to explore the relationships  
432 between two fundamental properties of the OM, its origin and its quality. A positive relationship  
433 between DI and EHAA/THAA ratio has been previously evidenced supporting the idea that as OM is  
434 degraded in the sediments, it becomes less available to enzymes (Dauwe et al., 1999b). Here, the  
435 reverse relationship was observed with a significant negative correlation between DI and EHAA/THAA  
436 ratio. The mixing of different pools of terrestrial OM may explain these opposite results. A study focusing  
437 on the benthic food web in a Mediterranean lagoon has revealed that different types of plants displayed  
438 contrasted levels of bioavailability with terrestrial plants exhibiting low EHAA/THAA ratios (10.4-18.1%),

439 seagrasses having intermediary values (12.2-33.4%), and salt marsh vegetation representing a highly  
440 digestive source of OM (50.0-60.2%) (Carlier et al., 2007). In good agreement with these earlier results,  
441 macrodetritus isolated from sediments at the MESURHO station have a low digestibility (EHAA/THAA  
442 ratio = 9.8) and a DI value (0.29) in the range of those calculated for the layers enriched in plant detritus  
443 (Pruski, unpublished result). As a general trend bioavailability was thus higher when the contribution of  
444 plant detritus was lower ( $r^2=0.85$ ). Consequently, the lower bioavailability observed in February, April  
445 and some layers from August may be attributed to the presence of macrodetritus. There was also a  
446 positive correlation between the DI and the proportion of fatty acids specific of epicuticular waxes from  
447 leaves (LC-SAFA) indicating that macrodetritus represent in our system a source of fresh OM, and that  
448 LC-SAFA are good tracers of litter inputs (i.e. they are less abundant in soils than in the litter).

449 In the flood deposit, soils certainly account for most of the particulate OC exported to the  
450 prodelta as observed previously after the flood of June 2008 (Cathalot et al., 2013). This hypothesis is  
451 supported by low contributions of biomarkers of phytoplankton and higher plant detritus. The different  
452 indexes of degradation provide contrasted insights on the history of this material. The low values of the  
453 amino acid based degradation indexes (DI and RI) indicate that the POC exported during the June flood  
454 was more degraded than the material delivered during periods of normal river regime (Bourgeois et al.,  
455 2011). This is consistent with the weathering of degraded POM from soils or riparian areas during  
456 intense rainfall events and the decrease of benthic microbial remineralisation (lower DOU in July and  
457 August, Table 2). However, the flood deposit was also characterised by high EHAA/THAA ratios (on  
458 average 32% in the flood deposit versus 23% in the February and April cores). The higher bioavailability  
459 of this material is somewhat counterintuitive. One would expect soil OM to be less prone to enzymatic  
460 digestion than fresh detritus. From this point of view, the particulate matter transferred to the sea  
461 during the 2008 and 2010 high-discharge events differed remarkably (EHAA/THAA ~20% in 2008,  
462 Bonifácio et al., 2014). In 2008, strong rainfalls were responsible for the opening of the spillway of the  
463 Serre Ponçon dam (Marion et al., 2010). Silts were eroded from black marls of the Durance watershed.  
464 As a consequence, this material was old and refractory ( $\Delta^{14}C = -495.1\text{‰} \pm 1.7$  in Cathalot et al., 2013;

465 DI= -0.13, Bourgeois unpublished result). Differences in bioavailability between the TSM delivered  
466 during the 2008 and 2010 events may be related to the watersheds affected by the precipitation and  
467 the nature of the material transported. Low pigment concentrations in the material exported in June  
468 2010 (Fagervold et al., 2014) indicate that EHAA were mostly associated to non-algal OM, and certainly  
469 incorporated to geopolymers as humic substances (Burdige and Martens, 1988). The exported SPM  
470 furthermore contained two pools of OM with distinct amino acid compositions: the first and dominant  
471 pool was more degraded than the OM delivered during periods of normal discharge (negative DI of the  
472 THAAs  $-0.02 \pm 0.03$ ), while another minor fraction of the OM was more labile as shown by elevated DI  
473 values calculated on the EHAA ( $DI_{EHAA} \sim 0.33 \pm 0.01$  for the flood deposit).

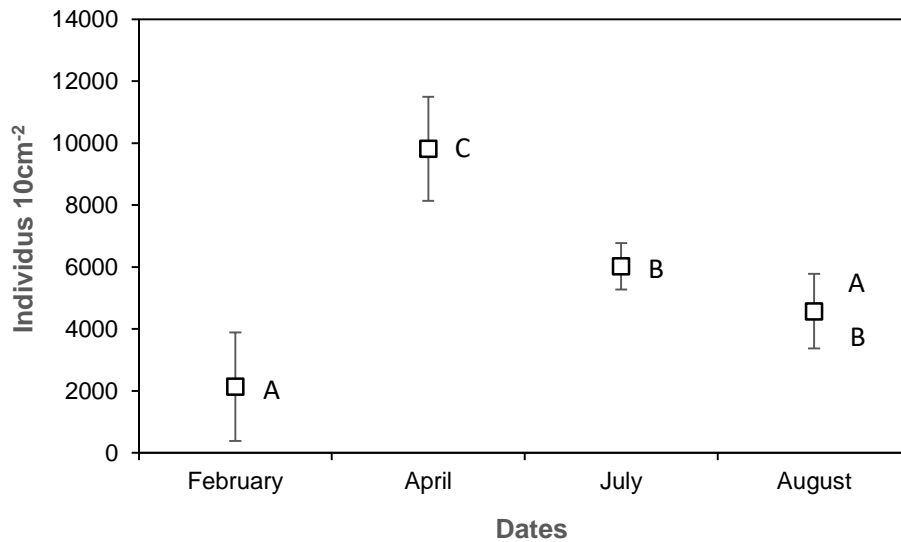
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### 475 **3.5. Temporal changes in meiofaunal community**

476 Meiofaunal abundances increased from February ( $2137 \pm 1401$  ind.  $10 \text{ cm}^{-2}$ ) to April ( $9818 \pm$   
477  $2027$  ind.  $10 \text{ cm}^{-2}$ ) with intermediate abundances in July ( $6025 \pm 1375$  ind.  $10 \text{ cm}^{-2}$ ) and August ( $4574 \pm$   
478  $1394$  ind.  $10 \text{ cm}^{-2}$ ) (Fig. 5). Nematodes were the most abundant metazoans (70%), followed by  
479 harpacticoid copepods (18%), annelids (4.5%), kinorhynchs (4%), foraminiferans (2%), cumaceans (1%)  
480 and turbellarians (0.5%) (Supplementary material, Table S2). This community structure was typical of  
481 soft bottom habitats (Danovaro et al., 2000; Giere, 2009; Moodley et al., 2000).

482 Total abundances of meiofauna (Fig. 5) were in the same range as those reported for other sites  
483 in the Gulf of Lion (de Bovée et al., 1990; Grémare et al., 2002). Differences between dates were  
484 statistically significant (one-way ANOVA,  $F=15.75$ ,  $p < 0.001$ ). Pairwise comparisons revealed  
485 significantly higher abundances in April and significantly lower in February (Tukey post hoc test,  
486 Supplementary material, Tables S3 and S4). The fivefold increase in the meiofaunal abundance from  
487 February to April coincided with the inputs of fresh and labile OM on the sea floor (enrichment in algal  
488 PUFA and amino acids, Fig. 3). Peaks of abundance are frequently observed after the post-bloom  
489 sedimentation of phytodetritus (Palacín et al., 1992; Vanaverbeke et al., 2004). Giere (2009) reported

490 that decaying phytoplankton results in the deposition of a fluffy layer of phytodetritus on the sediment  
491 and, after a short time (a few days), those unconsolidated organic deposits enhance the bacterial activity  
492 and cause a significant increase in meiofaunal abundance.

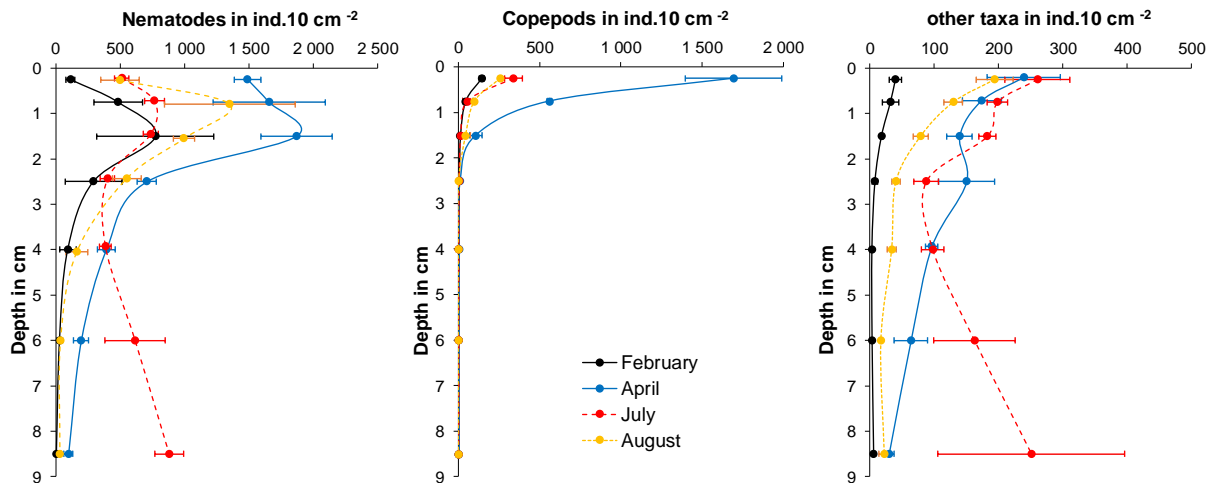


493  
494 **Figure 5: Total meiofaunal abundances at the MESURHO station in February, April, July, and August 2010.**  
495 Values are means  $\pm$  SD (n = 3 cores). Analysis of variance (one-way ANOVA,  $F=15.75$ ,  $p < 0.001$ ) and  
496 Tukey post hoc test, dates sharing the same letters are not significantly different.

497  
498 Results from the two-way ANOVA show the significant effect of sediment depth on the  
499 distribution of the meiofauna ( $F=26.87$ ,  $p < 0.001$ ). Significant “date x sediment depth” interaction terms  
500 ( $F=3.95$ ;  $p < 0.001$ ) furthermore indicate that the vertical distribution of the meiofauna differed  
501 between sampling periods (Table S5). In February, April and August, the vertical distribution of the  
502 meiofauna showed a typical pattern with high abundances near the surface (0-3 cm depth) and  
503 decreasing abundances with sediment depth (Fig. 6) as already described by Soetaert et al. (1995) and  
504 Vanreusel et al. (1995). The highest values were recorded on the first 2 cm of the cores, which  
505 corresponded to the layers of sediment enriched in phytodetritus (Fig. 3). This vertical pattern could be  
506 due to the active migration of the meiofauna to the food source accumulated on the sediment surface  
507 (Franco et al., 2008; Moens et al., 2013). Sediment oxygenation could be another regulating factor since

508 oxygen penetration in the sediment was very limited in the prodelta area (Fig. 2). Oxic niches were thus  
509 only available close to the sediment–water interface.

510



511

512 **Figure 6: Vertical distribution of meiofauna (nematodes, copepods and other taxa) at the MESURHO**  
513 **station in February, April, July and August 2010.** Values are means  $\pm$  SEM (n=3 cores). Note that some  
514 symbols were slightly shifted vertically relative to each other for visibility.

515

516 The vertical distribution of the meiofauna in July differed from the general pattern with high  
517 abundances in the deep layers similar to those recorded in the very upper layers of the other dates  
518 (two-way ANOVA,  $p < 0.001$ , Supplementary material, Table S5). The vertical profiles of copepods seem  
519 to fit the pattern of oxygen penetration depth (Fig. 2), but this clearly does not apply to nematodes and  
520 foraminiferans, which displayed the highest abundances in deep sediment layers (5 to 10 cm depth,  
521 Supplementary material, Table S2). These changes in the vertical distribution of the main meiofaunal  
522 taxa occurred just a couple of days after the flood of the Rhône tributaries and the sudden increase in  
523 TSM (Fig. 1). The drop in meiofaunal total abundance and the presence of a high density of nematodes  
524 in the deep layers after this high-discharge event can be explained by the burial of the meiobenthic  
525 community as observed experimentally with the simulated deposition of dredged material  
526 (Schratzberger et al., 2004). As so the present results corroborate the observation of Pelletier (1999)  
527 that high-discharge events severely affect the meiofauna with a reduction of its abundance. Among the



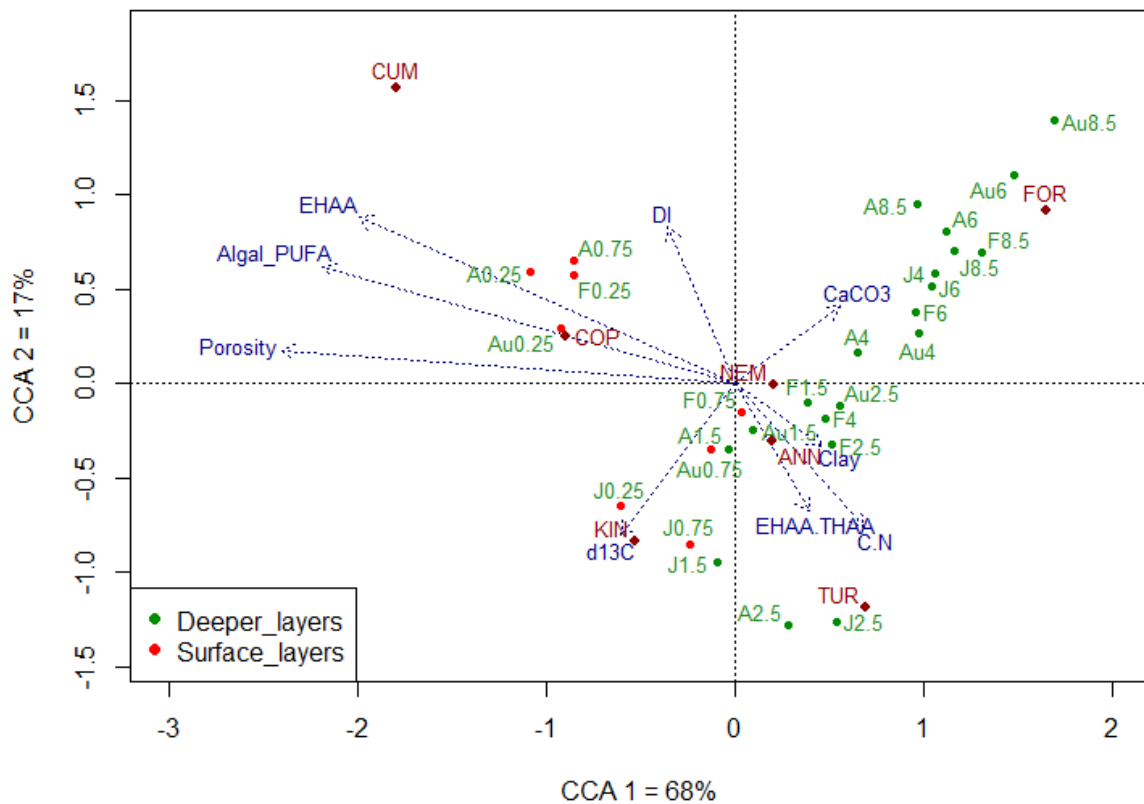
528 “other taxa” the clear dominance of foraminifera from genus *Leptohalysis* was noted in July. This  
529 foraminiferan is considered as an opportunistic taxon resistant to high turbidity, large inputs of  
530 terrestrially-derived OM, and low oxygen penetration in the sediment (Mojtahid et al., 2009; Scott et  
531 al., 2005). An opportunistic strategy allows *Leptohalysis* to proliferate in the Rhône prodelta in just a  
532 few days after a flood (Goineau et al., 2012).

533 In August, the community had already recovered a pre-disturbance structure. This short  
534 resilience time may be explained by a particularity of the study site. The Gulf of Lion is a highly  
535 hydrodynamic system, exposed to frequent strong winds and weather conditions where the benthic  
536 ecosystem undergoes frequent physical disturbance (Pont et al., 2002). High hydrodynamism can  
537 promote meiofaunal recolonisation. Indeed, while strong currents mechanically remove meiofauna  
538 from sediment, the first phases of recolonisation generally proceed very rapidly (1-2 weeks) after a  
539 severe devastation (review by Coull and Palmer, 1984; Schratzberger et al., 2004). The rapid dispersal  
540 of meiofauna has been ascribed primarily to water column processes, including passive erosion or active  
541 emergence (Armonies, 1994, 1988; Palmer et al., 1988; Palmer and Gusf, 1985), but the colonisation of  
542 defaunated sediments via lateral interstitial migration has also been observed (Schratzberger et al.,  
543 2004).

544

### 545 3.6. Linking meiofaunal composition and sediment properties

546 Canonical correspondence analysis (CCA) allows to relate the abundance of species to  
547 environmental variables (ter Braak, 1986). The canonical ordination diagram summarised the ecological  
548 preferences of the meiofaunal taxa at the MESURHO station (Fig. 7). This constrained ordination  
549 explained 54% of the total inertia. Permutation tests confirmed that relations between taxa abundances  
550 and sediment properties were statistically significant ( $p < 0.01$ ) for the sum of all canonical axes ( $F$  ratio  
551 = 2.3) and for the two first axes ( $F$  ratio = 14.9 and 4.2 for axis 1 and axis 2, respectively). Together, the  
552 first and second principal canonical axes accounted for 85% of the relationship between taxa and  
553 environmental parameters.



554

555 **Figure 7: Canonical correspondence analysis (CCA) triplot showing ordination of meiofaunal taxa at the**  
 556 **MESURHO site in February, April, July and August 2010 with environmental variables as arrows and**  
 557 **samples as dots.**

558 Nematodes (NEM), copepods (COP), kinorhynchs (KIN), annelids (ANN), turbellarians (TUR), cumaceans  
 559 (CUM), and foraminiferans (FOR). Environmental variables are C/N = molecular carbon to nitrogen ratio,  
 560  $\delta^{13}\text{C}$  = bulk stable isotope value, EHA: normalised concentration in enzymatically hydrolysable amino  
 561 acids, EHA/THAA: enzymatically hydrolysable amino acids to total hydrolysable amino acid ratio, DI=  
 562 degradation index, algal PUFA = normalised concentration in algal polyunsaturated fatty acids, clay=  
 563 proportion of clay,  $\text{CaCO}_3$  = calcium carbonate percentage, and porosity.

564 Sample code is as follow: the letter indicates the month (F= February, A= April, J= July, Au= August) and  
 565 the number corresponds to the mid-depth of the sediment layer (in cm). Red dots indicate surface  
 566 sediment layers (0-0.5cm and 0.5-1cm), and green dots deeper sediment layers (1-2cm, 2-3cm, 3-5cm,  
 567 5-7cm, and 7-10cm).

568

569           Among all the candidate environmental constraints, permutation tests showed that porosity,  
570 percentage of algal PUFA and normalised concentration of EHAA were the most influential on the  
571 meiofauna (Table 3). These three variables were strongly negatively correlated to the first axis, meaning  
572 that the main ecological gradient was linked to higher porosity and inputs of labile OM. DI was positively  
573 correlated to the second axis, whereas  $\delta^{13}\text{C}$ , C/N and EHAA/THAA were negatively correlated. With no  
574 surprise the meiofaunal community was mainly distributed along the first axis according to sediment  
575 depth, with negative scores for the surface layers (0-0.5 & 0.5-1 cm) and positive scores for deeper  
576 sediments (below 1cm). The meiofauna inhabiting the surface sediments further aggregated on the  
577 second axis according to the origin of the OM. As seen before, in February, April and August, fresh  
578 suspended particulate matter settled on the seafloor (Fig. 3). The meiofaunal community clearly  
579 responded to these inputs of food with higher frequencies of copepods and cumaceans (Fig. 7). A  
580 distinct community was found in July in the three first centimetres of the flood deposit. This community  
581 was related to higher  $\delta^{13}\text{C}$ , EHAA/THAA, and C/N ratios. Finally, communities from the deepest sediment  
582 layers (5-7 and 7-10cm) were grouped and were not related to any of the environmental factors  
583 examined in the present study.

584           The constrained ordination also displayed how the meiofaunal taxa were structured with  
585 respect to their environmental constraints and agreed well with the known ecological niches of the  
586 recorded taxa. Many cumaceans and harpacticoid copepods rely on planktonic diatoms sinking on the  
587 seafloor (De Troch et al., 2005; Giere, 2009; Higgins and Thiel, 1988). In good consistency with their  
588 feeding habits, cumaceans and copepods were related to inputs of fatty acids produced by  
589 phytoplankton and higher level of bioavailable amino acids found on the top of the cores. Kinorhynchs  
590 belong to another group with a known preference for the upper (0-3 cm) oxygenated surface layers  
591 (Giere, 2009). Shallow water forms feed mainly on diatoms, but they are also linked to organically  
592 enriched sediments (Higgins and Thiel, 1988) as those found near river mouths (Guidi-Guilvard and  
593 Buscail, 1995). As expected, kinorhynchs were found in the surface sediments, but they displayed high  
594 relative frequencies (~13%) in the flood deposit that recovered the seafloor in July. While kinorhynch

595 density in the top layers remained constant from April to August, copepod and cumacean densities  
596 dropped remarkably after the flood (Supplementary material, Table S2). This shows that crustaceans  
597 and kinorhynchs respond differently to river regime. In a mesocosm study, Rudnick (1989) found that  
598 copepods and kinorhynchs belong to two distinct feeding groups; the first group consuming fresh OM,  
599 while the second one could use older detrital matter. However, since the sampling only occurred a few  
600 days after the flood, it seems unlikely that the nature of the available OM could be the factor affecting  
601 meiofaunal community in July. Kinorhynchs can perform vertical movements in the sediment  
602 (Shimanaga et al., 2000). A higher capacity to migrate upward and colonise the newly flood deposit  
603 could explain the apparent resilience of kinorhynchs to the physical perturbation induced by the high-  
604 discharge event. Nematodes and annelids were the taxa whose occurrence and variability in density  
605 were the less explained by the CCA. Free-living nematodes, the metazoans with the greatest species  
606 richness in the sediments, occupy various ecological niches with different trophic requirements and  
607 sediment preferences (Giere, 2009; Moens et al., 2013), which may explain their wide vertical  
608 distribution. The ordination showed anyway their preference for subsurface and deeper sediment  
609 layers. Like nematodes, meiobenthic annelids are euryoecious, their preferences relate to sediment  
610 structure and organic content (Giere, 2009; Villora-Moreno, 1997). In the present study, they were  
611 related to ascending EHAA/THAA and C/N ratios. Foraminiferans were associated with deeper sediment  
612 layers and CaCO<sub>3</sub>. Most foraminiferans are versatile for microhabitat selection, food supply and oxygen  
613 availability. Mojtahid et al. (2010) investigated microhabitat preferences of living foraminiferans in front  
614 of the Rhône River mouth. They found two different assemblages: infaunal species with maximum  
615 densities in anoxic layers were dominant close to the river mouth, while species living predominantly in  
616 the top surface layer dominated in areas less influenced by fluvial inputs. They postulated that the  
617 higher tolerance of infaunal species for degraded terrestrial OM explains their dominance in the  
618 prodelta area. This is consistent with the CCA ordination showing that foraminiferans were related to  
619 rather low  $\delta^{13}\text{C}$  (meaning higher contribution of terrestrial OM). Finally, turbellarians, a group with  
620 predatory habits or feeding on diatoms, only occurred in two samples (layers 2-3 cm in April and July).

621 Hence, little can be said of their ecological optimum. However, their occurrence is generally determined  
622 by the sediment water and oxygen contents (Giere, 2009).

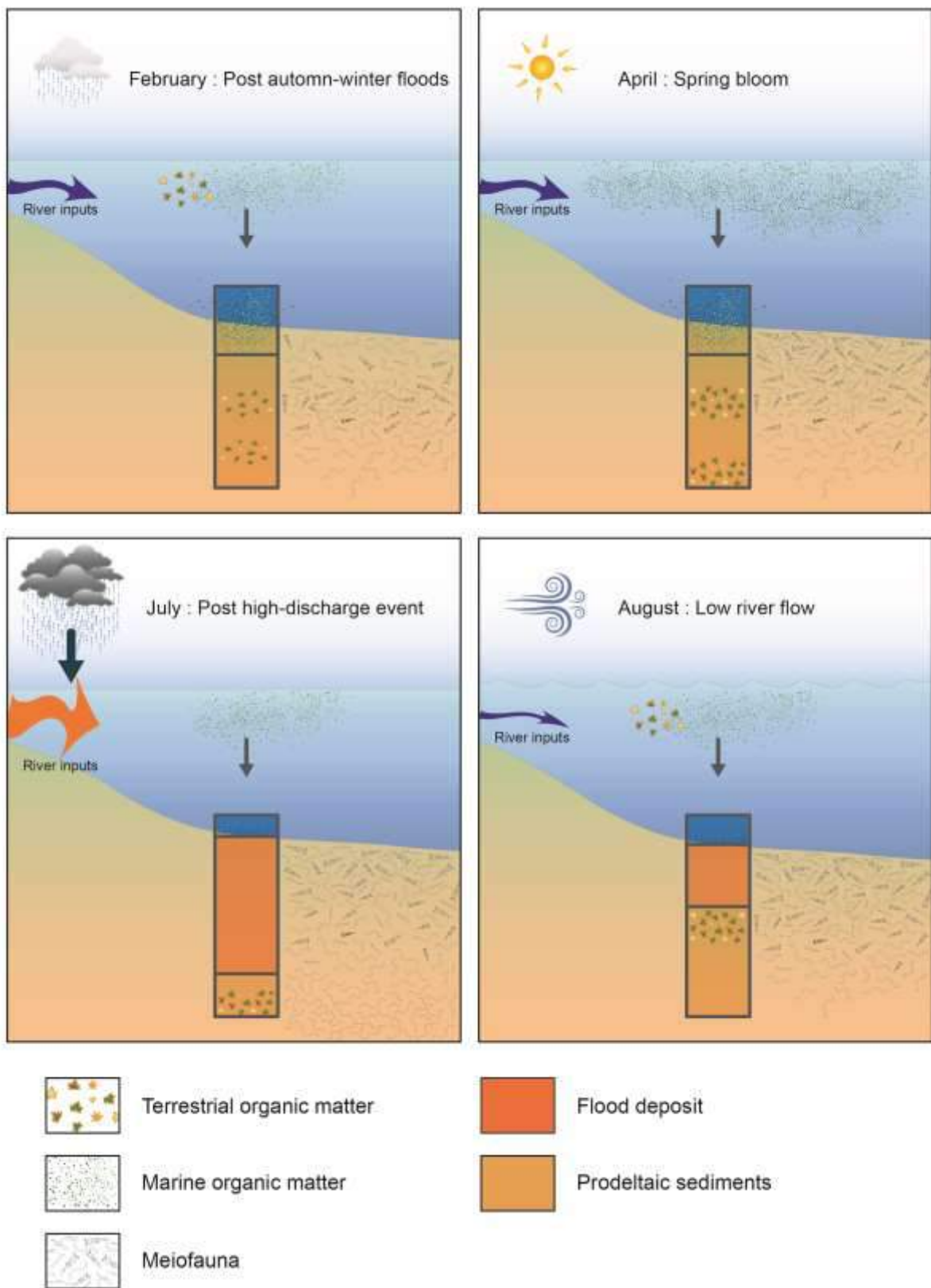
623 The CCA highlighted that the main ecological gradients for the meiofaunal community in the  
624 Rhône prodelta were related to sediment depth and river regime. Strong vertical patterns are found in  
625 recent sediments with the degradation of the most labile organic components and short-scale variations  
626 of abiotic parameters (oxygenation, redox potential...). These vertical patterns constrain the distribution  
627 of the meiofauna (Maria et al., 2012). In contrast, river regime accounts for temporal changes in the  
628 amount, provenance and nature of the OM accumulated in the prodelta (Cathalot et al., 2010). The  
629 relationships between the meiofauna and the biochemical characteristics of sedimentary OM have been  
630 previously investigated by de Bovée et al. (1990) and Grémare et al. (2002) in the Gulf of Lion. They  
631 reported that meiofaunal abundance correlated better with concentrations in lipids and EHAA rather  
632 than with bulk properties of the OM (nitrogen and organic carbon contents) on the shelf (0 – 175 m  
633 depth range). In the present study, porosity, algal PUFA and EHAA were the best predictors of  
634 meiofaunal composition, whereas porosity,  $\delta^{13}\text{C}$  and DI was the best combination of explanatory  
635 variables (Table 3). The strong influence of porosity on the meiofauna is certainly indirect. This factor is  
636 related to sediment depth as many other environmental variables not measured in the present study.  
637 In particular, porosity partially controls important abiotic factors such as dissolved oxygen diffusion and  
638 thus redox potential (Eh). The present results furthermore show that qualitative descriptors of  
639 sedimentary organics not only explain spatiotemporal changes in meiofaunal composition (de Bovée et  
640 al., 1990; Grémare et al., 2002), but also temporal changes in the vertical distribution of meiofaunal  
641 taxa.

642

#### 643 4. Conclusions

644 Major variations of the origin and quality of sedimentary OM are observed in the Rhône River  
645 prodelta at a monthly time scale. These fluctuations are mainly controlled by the fast dynamic of the  
646 processes affecting river flow and inputs from the watershed, but also by biological and physical

647 processes in the coastal area. Terrestrial organic inputs exported mostly during periods of high river  
648 discharge are preserved in the sediments until further remobilisation (Fig. 8). High-discharge events in  
649 autumn and winter mostly bring a material enriched in plant detritus, while other events as the one  
650 triggered by intense rainfalls in June 2010 are responsible for the transport of more degraded and poorly  
651 reactive POC. These different pools of OM (soil, litter, phytodetritus), with variable composition and  
652 quality, constitute a variety of trophic resources for the infauna. In this very complex and dynamic  
653 system, the meiofaunal community is driven by both trophic conditions and deposition of new sediment  
654 layers linked to the hydrological regime of the Rhône River. Inputs of high quality OM (highlighted by  
655 fatty acid biomarkers and amino acid indices) appear as a key structuring factor for the meiofauna as  
656 already showed by Vanreusel et al. (1995) and Giere (2009). Meiofauna is more abundant in spring when  
657 the sedimentation of labile OM originating from the phytoplankton bloom induced eutrophic  
658 conditions, whereas meiofaunal densities are low in late summer due to reduced inputs of labile POC  
659 (Fig. 8). The current results also point out the rapid response of the meiofauna to a short high-discharge  
660 event and the higher importance of analysing the vertical distribution of meiofaunal taxa rather than  
661 the total meiofauna abundances, since it was more relevant to show the perturbation. The meiofauna  
662 was severely impacted by this physical disturbance with a significant decrease of its total density and  
663 the burial of the meiobenthic community under the flood deposit, even though the newly settled layer  
664 was rapidly colonised (less than 2 months). The fast recovery of the meiobenthic community highlights  
665 that the meiofauna accounts for a highly resilient component of the benthic ecosystem in the vicinity of  
666 the Rhône River mouth, in contrast to the macrofauna, which is much longer affected by high-discharge  
667 events (Bonifácio et al., 2014).



668

669 **Figure 8:** Synthetic scheme of the processes influencing the dynamic of organic matter and meiofaunal  
 670 community composition during the four investigated periods in the Rhône prodelta.

671

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- 1024

1025 Table 1: Principal descriptors used in this study with their interpretation.

| Descriptors           | Feature        | Main diagnostic information   | References   |
|-----------------------|----------------|---|--|
| C/N                   | Source/Quality | Marine derived OM (6-9), Soil derived OM (8-20) and higher plants (>20); may decrease during OM decomposition           | Moloney and Field (1991), Hedges and Oades (1997), Meyers (1997)       |
| $\delta^{13}\text{C}$ | Source         | Marine OM ( $-20.1 \pm 0.8\text{‰}$ ) and Rhône River inputs ( $-27.1 \pm 0.6\text{‰}$ )                                | Harmelin-Vivien et al. (2008) and Higuera et al. (2014)                |
| DI                    | Quality        | Diagenetic alteration of OM with DI values ranging from $-2.2$ extensively degraded sediments to $-1.5$ for fresh algae | Dauwe et al. (1999b)   |
| RI                    | Quality        | Selective degradation during diagenesis and production of non-proteic amino acids, lower values in degraded sediments   | Jennerjahn & Ittekkot (1997)   |
| EHAA/THAA (%)         | Quality        | OM bioavailability for the benthic fauna ranging from 0 to 100%   | Mayer et al. (1995)  |
| MC-SAFA               | Source         | Mixed origin, but shorter chains predominate in phytoplankton   | Dunstan et al. (1994), Bianchi and Canuel (2011)                       |
| LC-SAFA               | Source         | Terrestrial higher plants, macrodetritus  | Bianchi and Canuel (2011), Dunstan et al. (1994), Pruski et al. (2015) |
| Ter PUFA              | Source         | Terrestrial higher plants (>2.5%)   | Budge et al. (2001), Pruski et al. (2015)                              |
| Algal PUFA            | Source         | Phytoplankton with $\text{C}_{20:5\omega3}$ specific of diatoms   | Dunstan et al. (1994)  |
| MUFA                  | Source         | Mixed origin with $\text{C}_{16:1\omega7}$ common in diatoms and bacteria   | Bianchi and Canuel (2011), Dunstan et al. (1994)                       |
| BAFA                  | Source         | Bacterial sources   | Bianchi and Canuel (2011)  |

1026 The degradation index (DI), reactivity index (RI) and enzymatically hydrolysable amino acids to total hydrolysable amino acids ratio (EHAA/THAA) are  
 1027 inferred from the amino acid composition. Fatty acid biomarkers are grouped as follows: mid-chain even-number saturated fatty acids with less than 20  
 1028 carbons (MC-SAFAs), long-chain saturated fatty acids with 24 carbon or more (LC-SAFA), polyunsaturated fatty acids with 18 carbons ( $\text{C}_{18:2\omega6}$  and  $\text{C}_{18:3\omega3}$ ,  
 1029 Terr PUFA), the remaining PUFA attributed to microalgae (Algal PUFA), the monounsaturated fatty acids (MUFA) and the straight and branched odd-  
 1030 numbered fatty acids of bacterial origin (BAFA). The unsaturation index is calculated as the sum of products of the number of double bonds of each acid  
 1031 multiplied by its percentage of the total fatty acid composition.

1032

1033 Table 2: Temporal variations of Diffusive Oxygen Uptake (DOU) rates in the sediments of the Rhône River  
1034 prodelta in April, July and August 2010. Values are means  $\pm$  standard deviations (n= 4), nd= not  
1035 determined.

1036

| Stations | DOU            |                |             |
|----------|----------------|----------------|-------------|
|          | April 2010     | July 2010      | August 2010 |
| MESURHO  | 16.9 $\pm$ 4.1 | 10.1 $\pm$ 0.6 | 9 $\pm$ 1.5 |
| A        | 14.9 $\pm$ 1.3 | 10.6 $\pm$ 3.6 | nd          |
| AK       | 19.7 $\pm$ 3.5 | 11.4 $\pm$ 1.3 | nd          |
| B        | 12.7 $\pm$ 2.1 | 11.3 $\pm$ 2.9 | nd          |
| K        | 14.9 $\pm$ 2.6 | 11.8 $\pm$ 4.9 | nd          |

1037

1038



1039 **Table 3:** Marginal and conditional effects of environmental variables determined using forward selection. Ranking is based on their P-value and Akaike  
 1040 Information Criterion (AIC) where the variable with the lowest AIC value is the most influential. 999 permutations. Significant variables are indicated in  
 1041 bold, \* p<0.05, \*\* p<0.01. Best combination of variables: Porosity +  $\delta^{13}\text{C}$  + DI.  
 1042

1043

| Marginal effects |                       |        |         |        | Conditional effects |          |   |         |        |       |    |
|------------------|-----------------------|--------|---------|--------|---------------------|----------|---|---------|--------|-------|----|
| Rank             | Variable              | AIC    | F ratio | Pr(>F) | Rank                | Variable | AIC                                     | F ratio | Pr(>F) |       |    |
| 1                | <b>Porosity</b>       | 79.935 | 7.267   | 0.005  | **                  | 1        | <b>Porosity</b>                         | 79.935  | 7.267  | 0.005 | ** |
| 2                | <b>Algal PUFA</b>     | 81.865 | 5.0518  | 0.005  | **                  | 2        | <b><math>\delta^{13}\text{C}</math></b> | 78.509  | 3.2544 | 0.015 | *  |
| 3                | <b>EHAA</b>           | 81.042 | 5.9774  | 0.015  | **                  | 3        | <b>DI</b>                               | 77.785  | 2.4517 | 0.045 | *  |
| 4                | C/N                   | 85.621 | 1.1536  | 0.270  |                     | -        | EHAA                                    | 78.170  | 1.3657 | 0.180 |    |
| 5                | $\delta^{13}\text{C}$ | 85.715 | 1.0625  | 0.385  |                     | -        | Clay                                    | 78.285  | 1.2658 | 0.290 |    |
| 6                | EHAA/THAA             | 86.120 | 0.6742  | 0.575  |                     | -        | Algal PUFA                              | 78.507  | 1.0746 | 0.400 |    |
| 7                | DI                    | 86.174 | 0.6229  | 0.605  |                     | -        | EHAA/THAA                               | 79.305  | 0.3983 | 0.795 |    |
| 8                | CaCO <sub>3</sub>     | 86.252 | 0.5482  | 0.655  |                     | -        | CaCO <sub>3</sub>                       | 79.301  | 0.4013 | 0.820 |    |
| 9                | Clay                  | 86.343 | 0.4626  | 0.715  |                     | -        | C/N                                     | 79.419  | 0.303  | 0.925 |    |

1044