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

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Abstract:

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

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

1. Introduction

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

Deltas are peculiar estuaries that form where sand and mud supply exceeds sediment dispersal. Their existence and functioning are therefore closely linked to river inputs (Giosan et al., 2014). A plethora of river delta systems have formed in the microtidal wave-influenced setting of the Mediterranean Sea (Besset et al., 2017). The watersheds and fluvial regime of most Mediterranean deltas, including the Ebro, Rhône, Po and Nile, have undergone severe modifications to accommodate human activities (Day et al., 2019a). Despite considerable efforts to control the runoff of these rivers, the export of particulate matter takes place primarily during high discharge flood events triggered by intense rainfalls or oceanic storms (Antonelli et al., 2008). Depending on the season and drainage basin affected, the magnitude and nature of the particulate organic matter (POM) exported during these events are highly variable with inputs of fossil OC, eroded soils, riparian vegetation or phytoplankton (Antonelli et al., 2008; Cathalot et al., 2013; Harmelin-Vivien et al., 2010; Higueras et al., 2014; Marion et al., 2010; Tesi et al., 2008). Meteorological and hydrological drivers are thus expected to control the supply and quality of the POM delivered to the shelf as well as its bioavailability for the benthic fauna. Moreover, extreme flooding events results in the rapid deposition of fine terrigenous particles which have significant effects on the structure and function of macrobenthic communities (Cardoso et al., 2008; Lohrer et al., 2004; Norkko et al., 2002). For instance, off the Rhône River, the proliferation of opportunist species taking advantage of flood deposits has been observed in the months following major events (Salen-Picard et al., 2003). A very tight and complex relationship links river dynamic and macrofaunal communities in Mediterranean deltas (Akoumianaki and Nicolaidou, 2007; Bonifácio et al., 2014; Hermand et al., 2008; Salen-Picard et al., 2003). By contrast, meiobenthic communities (animals retained between 40 µm and 1 mm mesh size of sieves; Giere, 2009) from deltaic systems have received little attention (Danovaro et al., 2000; Guidi-Guilvard and Buscail, 1995; Palacín et al., 1992, Semprucci et al., 2019) at the notable exception of foraminiferans (Fontanier et al., 2008; Franzo et al., 2019; Goineau et al., 2012). The meiofauna has an important role in the functioning of benthic ecosystem, contributes significantly to the diet of many other animals (Coull, 1990), and facilitates mineralisation of organic material (Coull, 1999; Gee, 1989; Riera and Hubas, 2003). Because of their small size, lack of larval stage and shorter generation time, meiobenthic organisms respond more successfully than the macrofauna to changes in environmental conditions (Balsamo et al., 2012). As such, meiofaunal communities have been widely used to monitor the effects of both natural and anthropogenic perturbations in aquatic ecosystems (Coull and Chandler, 1992; Gambi et al., 2003; Schratzberger and Ingels, 2018, Semprucci et al., 2018). Although the meiofauna appears as a good bioindicator of organic enrichment and physical disturbance in coastal areas (Gambi et al., 2003), there is a paucity of studies focusing on their response to river inputs (Danovaro et al., 2000; Guidi-Guilvard and Buscail, 1995; Palacín et al., 1992; Pelletier et al., 1999).

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

2. Materials and methods

2.1. Regional setting and study area

The Rhône River, now the main river in the Mediterranean Sea since the damming of the Nile, links the Rhône glacier in the Swiss upper Alps to the Camargue delta on the French coast of the Mediterranean Sea (the Gulf of Lion). It is mainly an Alpine river, which drains a relatively small (95,000 km^2), but highly diversified, watershed exhibiting a strong geological heterogeneity (Olivier et al., 2009). The Rhône catchment includes several climatic zones (mountainous, oceanic and Mediterranean) resulting in a very complex hydrological regime and a strong inter annual variability (Pont et al., 2002). Typical of Mediterranean rivers, the runoff of the Rhône is characterised by flooding events triggered by intense rainfalls in autumn and snowmelt in spring. As a consequence, solid export to the Gulf of Lion occurs mainly during short, but intense high-discharge events (Antonelli et al., 2008). Riverine particulate inputs undergo a rapid deposition near the river mouth in the prograding prodelta (Maillet et al., 2006). The unconsolidated sediments are frequently resuspended by episodes of strong winds or by near bottom currents (Ulses et al., 2008). The study area is located at 2.5 km of the Rhône River mouth in the prodelta area (Fig. 1).

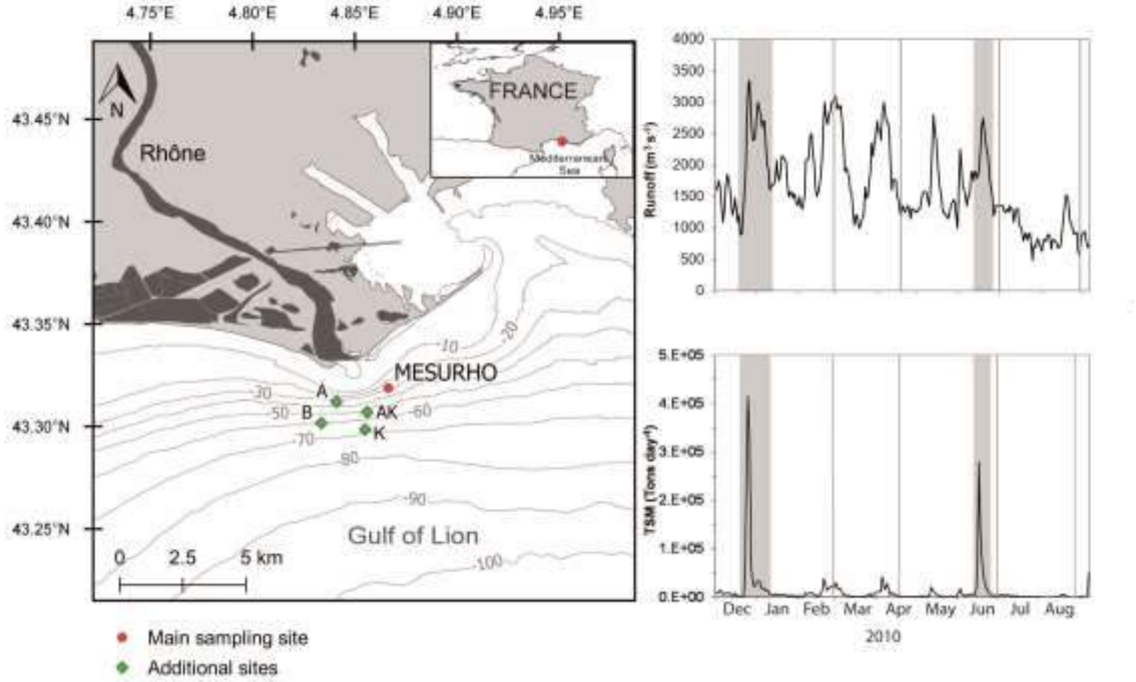

Figure 1: Location of the sampling sites in the Gulf of Lion (left) and Rhône River runoff and total suspended matter (TSM) concentration for 2010 (right). Rhône data were measured at the SORA Observatory Station in Arles, the most downstream gauge station, 40 km upstream the mouth. The vertical bars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

2.2. Hydrological and climatic conditions

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

2.3. Sediment sampling

The sampling targeted four contrasted periods in 2010: winter (20th February), spring (18th April), early (1st July) and late summer (28th August). Sediment cores were collected at station MESURHO (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 (Oktopus GmbH) during the field campaigns MESURHOBENT 1, 2, 3 and 4 (Rabouille, 2010a, b, c, d). At each sampling date, four undisturbed sediment cores (9.5 cm of diameter and 60 cm of height) were 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 cm). Since previous studies in the prodelta area have shown that variability among cores was low (Bourgeois et al., 2011; Cathalot et al., 2010; Pastor et al., 2011a), one core was conditioned in this study for sediment characterisation. Sediment layers were carefully homogenised, distributed in two aliquots and immediately frozen at -20°C. Sediment layers from the three other cores were preserved in 70% alcohol for meiofaunal analysis. Visual observation of the sediment cores used in this study showed no signs of burrows, biogenic structures, oxic voids or large macrofauna, suggesting low bioturbation activity.

2.4. Assessment of sediment characteristics

Sediment granulometry was assessed using a Malvern® Mastersizer 2000 laser diffraction particle size analyser. Porosity (ϕ) was calculated by determining water mass loss during drying assuming a value of 2.63 $g.cm^{-3}$ for grain size density and 1.03 $g.cm^{-3}$ for pore water density. Sediment granulometry, and porosity were determined in triplicate for each sample.

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

Enzymatically hydrolysable amino acids (EHAA), which correspond to the fraction of amino acids assumed to be bioavailable for benthic deposit-feeders, were extracted by the biomimetic approach of Mayer et al. (1995). THAAs and EHAAs were analysed by reverse phase high-performance liquid chromatography (HPLC, Gynkotek-Dionex system) following precolumn derivatisation with orthophtaldialdehyde (Lindroth and Mopper, 1979). The isoindol derivatives were separated on a C18-HPLC column using a non-linear gradient of methanol-acetate buffer and were detected by fluorescence at 450 nm using an excitation wavelength of 335 nm (Bourgeois et al., 2011).

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

2.5. Assessment of meiofaunal abundance and taxonomic composition

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

2.6. In situ microprofiling of dissolved oxygen and DOU calculation

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

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

Four oxygen microelectrodes were simultaneously deployed, and vertical depth profiles were measured with a 200 µm resolution together with a resistivity electrode. As their response to variations in oxygen concentrations is linear (Boudreau and Jorgensen, 2001), the O_2 microelectrodes were calibrated with a two-point calibration technique using the bottom water O_2 concentration determined by Winkler titration and the anoxic pore waters. Signal drift of O_2 microelectrodes during profiling was checked to be less than 5 %. Diffusive oxygen uptake (DOU) rates were calculated using Fick's first law (Berner, 1980, Eq. 3),

$$DOU = -\emptyset \cdot D_s \cdot \frac{d[O_2]}{dz}\bigg|_{z=0} \qquad (3)$$

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

2.7. Data analysis

The amount, sources, and quality of the sedimentary organic matter (OM) in the Rhône prodelta were assessed with a suite of bulk and molecular descriptors. The list of the parameters used in this study is provided in Table 1 with their interpretation. The degradation index (DI) was calculated from the molar composition of the THAA hydrolysates (Dauwe et al., 1999a). This index synthesises subtle changes in the amino acid composition linked with diagenesis into a univariate variable indicative of OM degradation stage, whose value decreases with increasing degradation. We applied the same calculation on the EHAA composition of the flood deposit. In this case, the index (DI_{EHAA}) provided information on the degradation stage of the pool of amino acids that may be assimilated by benthic organisms. The reactivity index [RI=(tyrosine+phenylalanine)/(β-alanine+ɣbutyric acid)] is another indicator of OM degradation (Jennerjahn and Ittekkot, 1997). It takes into account two opposite trends: the reactive aromatic amino acids, tyrosine and phenylalanine, are rapidly degraded in decaying OM, whereas their decarboxylation products, β-alanine and ɣ-butyric acid, consistently increase with microbial degradation (Alkhatib et al., 2012; Jennerjahn and Ittekkot, 1997).

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

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

Relationships between the abundance of meiofaunal taxa and factors, representing sediment characteristics, were summarised using a Canonical Correspondence Analysis (CCA) (ter Braak, 1986) performed with the R package 'vegan' (Oksanen et al., 2016). CCA allowed to simultaneously visualise the abundances of the principal meiofaunal taxa, the optimal niches (sample corresponding to sediment depth × date) with the environmental parameters (Borcard et al., 2011). The environmental variables identified by PCA were first retained. The "vif.cca" function of 'vegan' was then used to identify redundant constraints (i.e. environmental variables with variance inflation factors >10) and were removed from the analysis to reduce collinearity. CCA was finally performed on square root transformed abundances to reduce the weight of abundant taxa and a subset of standardised environmental variables describing the quality of food available for the meiofauna (δ^{13}C, C/N ratio, normalised concentration in EHAA, EHAA/THAA ratio, DI, % Algal PUFA) or related to sediment properties (porosity, % clay, and $CaCO_3$). The statistical significance of the overall relationship and of the canonical axes were evaluated using Monte Carlo permutation tests (999 permutations). The CCA ordination diagram displayed samples and taxa as points and environmental variables as vectors (Borcard et al., 2011). Finally, the relative importance of the explanatory variables was evaluated by forward selection followed by Monte Carlo permutation tests (999 permutations) using the "ordistep" function of 'vegan' (Blanchet et al., 2008). With this method, all variables are ranked on the basis of their marginal effects (i.e. considering each variable as the sole constraining variable) and conditional effects (i.e. forward selection on the best descriptors and evaluation of the fit of each variable in conjunction with the variable(s) already selected).

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

3. Results and discussion

3.1. Hydrological and climatological conditions

In 2010, the French Mediterranean coast experienced a cold and rainy winter with strong winds dominated by Mistral. Rains were frequent, but moderate with Rhône water discharge reaching 2500m^3 s^{-1} ten days before February sampling and 3000m^3 s^{-1} on the sampling date (Fig. 1). The organic content of the total suspended matter (TSM) was high (TOC= 7.81% on the 12th of February 2010, Kerhervé unpublished result). March was also rainy and windy. Two minor floods occurred before the April sampling, but TSM only slightly increased during these events. In April, the weather was fair with little wind and precipitation, but liquid discharge rates were high, possibly because of snow melting. As a consequence, TSM increased above 100mg.L^{-1}. On the 15th and 16th of June 2010, exceptional stormy rains (40cm per day) have generated severe flooding in south-eastern France. This rare and deadly flash flood event is believed to be the most important since 1827 (Payrastre et al., 2012). Rainfalls mostly affected the southeast tributaries of the Rhône River (the Durance, the Buëch, the Verdon, etc.) causing their overflow. The runoff of the Rhône River peaked at 2600m^3.s^{-1}, while solid discharge reached 2.8 10^5 tones on June 16, 2010. In the days before return to normal runoff, the Rhône brought approximately one fourth of the annual solid input for 2010. The summer was dry and hot. The daily runoff rate was below the mean inter annual flow rate of 1700 m^{3}s^{-1} and was typical of low river flow (500-1000 m^{3}s^{-1}). July was characterised by strong winds generally oriented N-NW (12 to 13 days of Mistral). The wind changed of direction on the 26th of July (S) and generated a storm regime. Meteorological conditions were similar on August with episodes of strong winds.

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

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

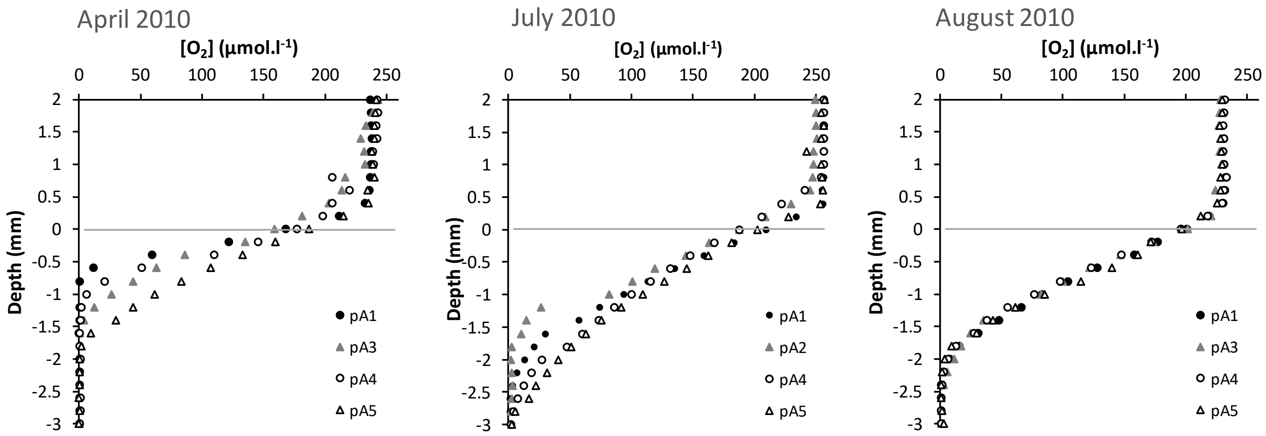

Figure 2: Dissolved oxygen microprofiles at the sediment-water interface recorded *in situ* at the MESURHO station in April, July, and August 2010. Each symbol represents a single electrode profile. The line at 0 mm indicates the sediment surface.

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

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

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

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

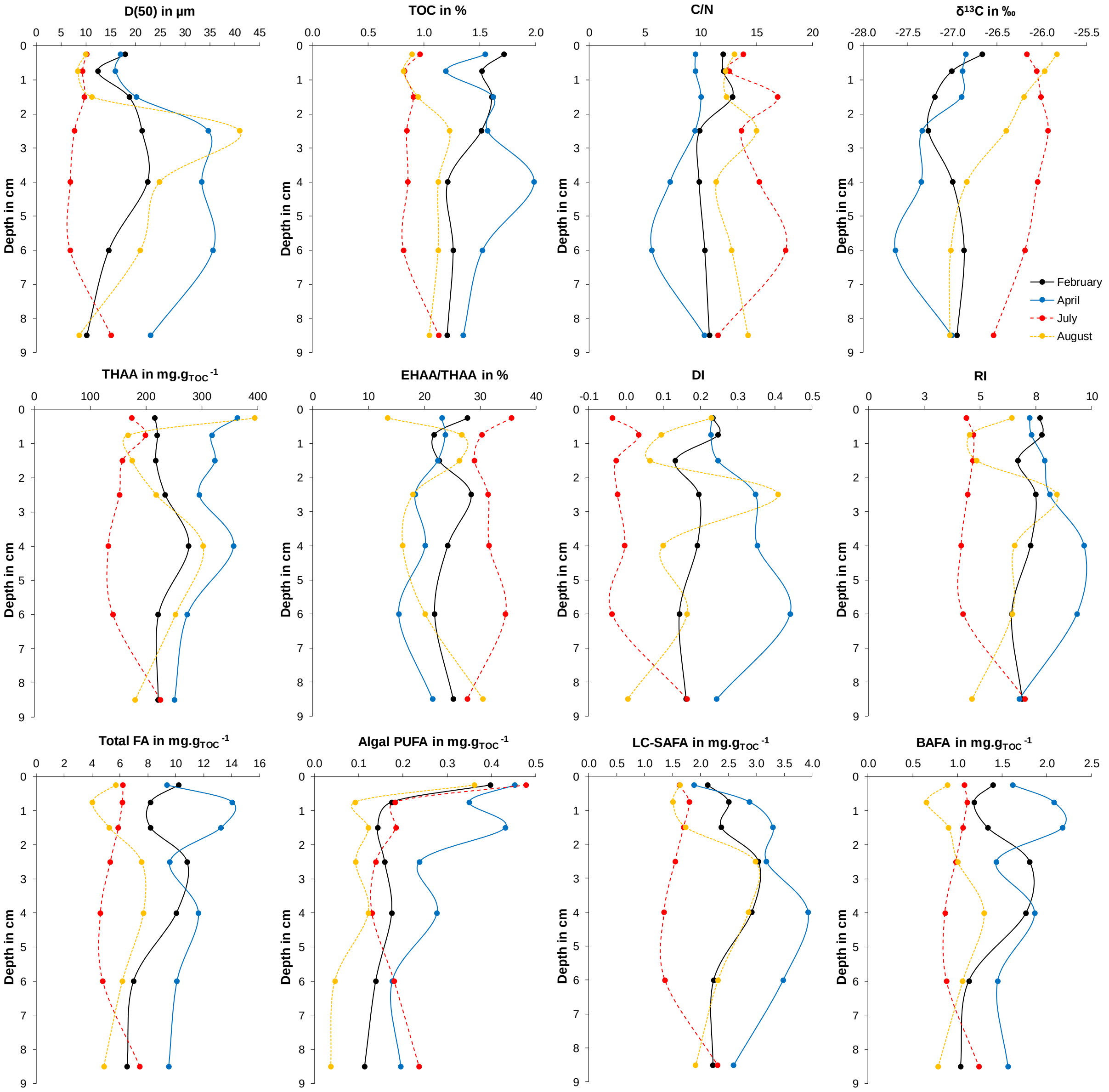

Figure 3: Down-core evolutions of sediment properties at the MESURHO station in February, April, July, and August 2010. D(50)= median grain size, TOC= total organic carbon, C/N= molecular carbon to nitrogen ratio, $\delta^{13}C$= bulk stable isotope value, THAA= normalised total hydrolysable amino acid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

In April, sedimentary characteristics were more heterogeneous on the 10cm layer than during the winter (Fig. 3). TOC content was still high and comparable to February in the surface sediment, but at 3-7cm depth, a layer enriched in markers of plant detritus was observed. At the surface, high concentrations in planktonic markers were again suggestive of phytoplankton inputs. Organic carbon, amino acids and fatty acids tended to be higher in the subsurface sediments. This coarser subsurface layer was also less degraded (higher DI and RI) with a lower bioavailability of the amino acid pool. Globally, this suite of descriptors indicates that plant detritus have been exported during the two floods that preceded the sampling, or that earlier deposits in the mud belt have been remobilised. Porosity was also discontinuous, in agreement with the successive deposition of different layers of material.

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

The trend for lower porosities at the end of August suggests that the summer conditions allowed the muddy deposits to settle and become more compact (Table S1, supplementary material). This is consistent with the concomitant stratification of the microbial community described by Fagervold et al. (2014) at this station. Organic content was still low, but OM characteristics indicate intense reworking of the sediments since July (Fig. 3). δ^{13}C values ranged from "flood signature" of the tributaries (~ -26‰) in surface to the usual winter value of the Rhône (~ -27‰). Below the first two centimetres, which kept the flood imprint, the sediment was enriched in TOC, amino acids, fatty acids, and long chain fatty acids. The down-core evolution of the DI is difficult to interpret. In the surface layer (0-0.5cm), the DI value was similar to values found in February and April on the top of the cores and may be indicative of the recent export of TSM by the Rhône River. Values for the 0.5-1 and 1-2cm layers were closed to those found in the flood deposit, between 2-3cm depth DI was similar to values measured in the April layer enriched with macrodetritus, and below DI was lower indicative of a more degraded pool of POM. Grain size followed the same trend as DI in good consistency with the hypothesis that the 2-3cm layer corresponded to sediments enriched in coarse macrodetritus. The proportion of bioavailable amino acids (EHAA/THAA) was also extremely variable along the sediment depth consistent with inputs of different sources of POM and non-steady state conditions.

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

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

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

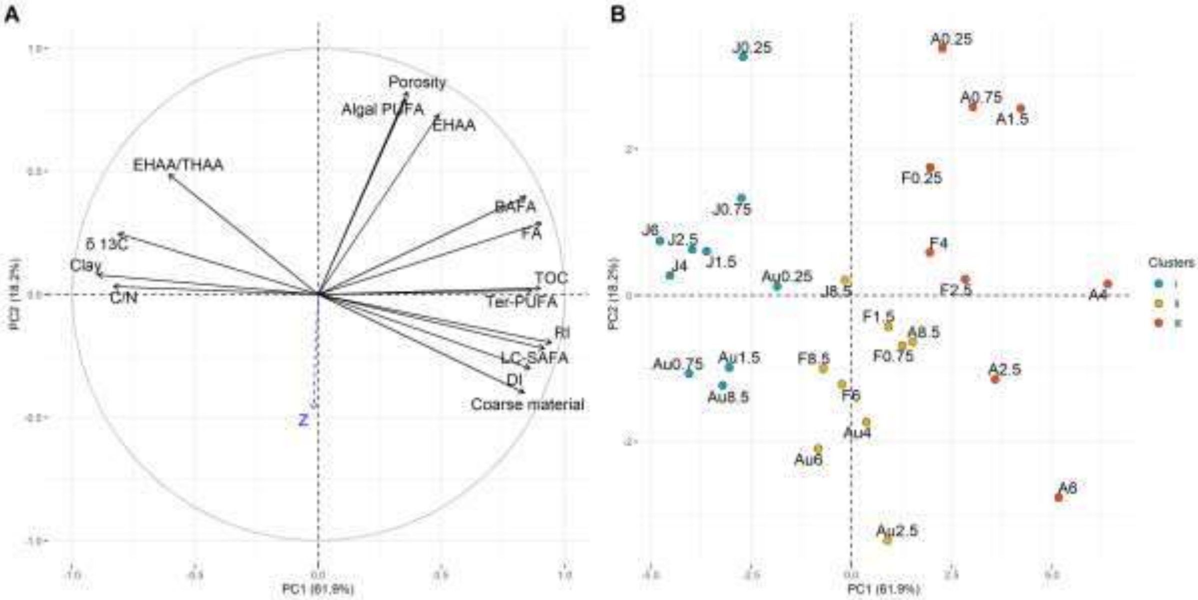

Figure 4: Principal component analysis (PCA) of sediments collected in the Rhône River prodelta: loading plot (A) and score plot (B) for the first and second principal components (7 sediment layers × 4 dates). Black arrows indicate active variables and the blue arrow corresponds to the supplementary variable (sediment depth: Z). Samples were clustered in 3 groups according to a hierarchical clustering analysis performed on the 5 first principal components of the PCA. Sample code is as follow: the letter indicates the month (F= February, A= April, J= July, Au= August) and the number corresponds to the mid-depth of the sediment layer (in cm). Clay= % of particles <4µm, Coarse material= % of particles >200µm, $CaCO_3$ = % of calcium carbonate. For all other variables see Table 1 for abbreviations. Concentrations in EHAA, fatty acids (FA), BAFA, LC-SAFA, Terrestrial PUFA & Algal PUFA were normalised to organic carbon content.

Results of the PCA show that sediment properties can be summarised in two independent principal components explaining 80% of the total variance (Fig. 4A). Sediment layers were not grouped by dates or strata on the two first components of the PCA (Fig. 4B), which is consistent with the successive deposition of particles originating from different sources. Two pools of organic inputs were clearly separated on the first component axis (PC1= 61.9 % of the total variance). A group of variables with positive loadings on PC1 characterised a coarser material enriched in TOC, fatty acids, and markers of vascular plants (LC-SAFA and Ter PUFA). This material also exhibited higher DI and RI values, indicative of limited diagenetic alteration, and depleted δ^{13}C values consistent with an input of modern plant detritus in C3 (δ^{13}C plant = -28‰, Hedges et al., 1986). Taken together, these results confirm that sediment cores collected in February and April 2010 were enriched in plant detritus (Fig. 4B, cluster II). A distinct source of OM associated to clay, low TOC content, higher C/N ratios and δ^{13}C values was found in June and some sediment layers in August 2010 (negative loadings on PC1 and cluster I). OM in the flood deposit (Cluster I) was also more bioavailable for the benthic fauna as seen by higher EHAA/THAA ratios (Fig. 3). The second principal component (PC2= 18.2% of the total variance) illustrates variations that can be attributed to sediment depth, such as the decrease in porosity in the sedimentary column and the rapid degradation of the most labile components (PUFA deriving from phytoplankton and EHAA). The distribution of layers from the April core along PC2 agrees with this general pattern: the 2 first centimetres (with positive loadings) being enriched in bioavailable OM, whereas the layers below (with negative loadings) contained a more refractory pool of OM. A second group of samples characterised by lower algal contents and porosity was also linked to PC2. This cluster regroups intermediate layers from August and some layers from February (cluster II on Fig. 4B).

The different molecular descriptors used in this study enable to explore the relationships between two fundamental properties of the OM, its origin and its quality. A positive relationship between DI and EHAA/THAA ratio has been previously evidenced supporting the idea that as OM is degraded in the sediments, it becomes less available to enzymes (Dauwe et al., 1999b). Here, the reverse relationship was observed with a significant negative correlation between DI and EHAA/THAA ratio. The mixing of different pools of terrestrial OM may explain these opposite results. A study focusing on the benthic food web in a Mediterranean lagoon has revealed that different types of plants displayed contrasted levels of bioavailability with terrestrial plants exhibiting low EHAA/THAA ratios (10.4-18.1%), seagrasses having intermediary values (12.2-33.4%), and salt marsh vegetation representing a highly digestive source of OM (50.0-60.2%) (Carlier et al., 2007). In good agreement with these earlier results, macrodetritus isolated from sediments at the MESURHO station have a low digestibility (EHAA/THAA ratio = 9.8) and a DI value (0.29) in the range of those calculated for the layers enriched in plant detritus (Pruski, unpublished result). As a general trend bioavailability was thus higher when the contribution of plant detritus was lower (r^2=0.85). Consequently, the lower bioavailability observed in February, April and some layers from August may be attributed to the presence of macrodetritus. There was also a positive correlation between the DI and the proportion of fatty acids specific of epicuticular waxes from leaves (LC-SAFA) indicating that macrodetritus represent in our system a source of fresh OM, and that LC-SAFA are good tracers of litter inputs (i.e. they are less abundant in soils than in the litter).

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

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

3.5. Temporal changes in meiofaunal community

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

Total abundances of meiofauna (Fig. 5) were in the same range as those reported for other sites in the Gulf of Lion (de Bovée et al., 1990; Grémare et al., 2002). Differences between dates were statistically significant (one-way ANOVA, *F*=15.75, $p < 0.001$). Pairwise comparisons revealed significantly higher abundances in April and significantly lower in February (Tukey post hoc test, Supplementary material, Tables S3 and S4). The fivefold increase in the meiofaunal abundance from February to April coincided with the inputs of fresh and labile OM on the sea floor (enrichment in algal PUFA and amino acids, Fig. 3). Peaks of abundance are frequently observed after the post-bloom sedimentation of phytodetritus (Palacín et al., 1992; Vanaverbeke et al., 2004). Giere (2009) reported that decaying phytoplankton results in the deposition of a fluffy layer of phytodetritus on the sediment and, after a short time (a few days), those unconsolidated organic deposits enhance the bacterial activity and cause a significant increase in meiofaunal abundance.

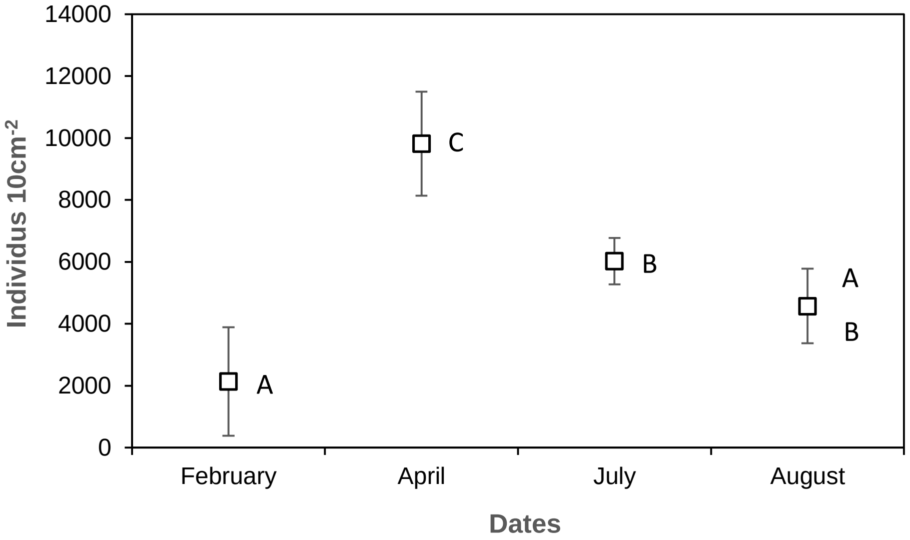

Figure 5: Total meiofaunal abundances at the MESURHO station in February, April, July, and August 2010. Values are means ± SD (n = 3 cores). Analysis of variance (one-way ANOVA, F=15.75, $p < 0.001$) and Tukey post hoc test, dates sharing the same letters are not significantly different.

Results from the two-way ANOVA show the significant effect of sediment depth on the distribution of the meiofauna (F=26.87, $p < 0.001$). Significant "date x sediment depth" interaction terms (F=3.95; $p < 0.001$) furthermore indicate that the vertical distribution of the meiofauna differed between sampling periods (Table S5). In February, April and August, the vertical distribution of the meiofauna showed a typical pattern with high abundances near the surface (0-3 cm depth) and decreasing abundances with sediment depth (Fig. 6) as already described by Soetaert et al. (1995) and Vanreusel et al. (1995). The highest values were recorded on the first 2 cm of the cores, which corresponded to the layers of sediment enriched in phytodetritus (Fig. 3). This vertical pattern could be due to the active migration of the meiofauna to the food source accumulated on the sediment surface (Franco et al., 2008; Moens et al., 2013). Sediment oxygenation could be another regulating factor since oxygen penetration in the sediment was very limited in the prodelta area (Fig. 2). Oxic niches were thus only available close to the sediment–water interface.

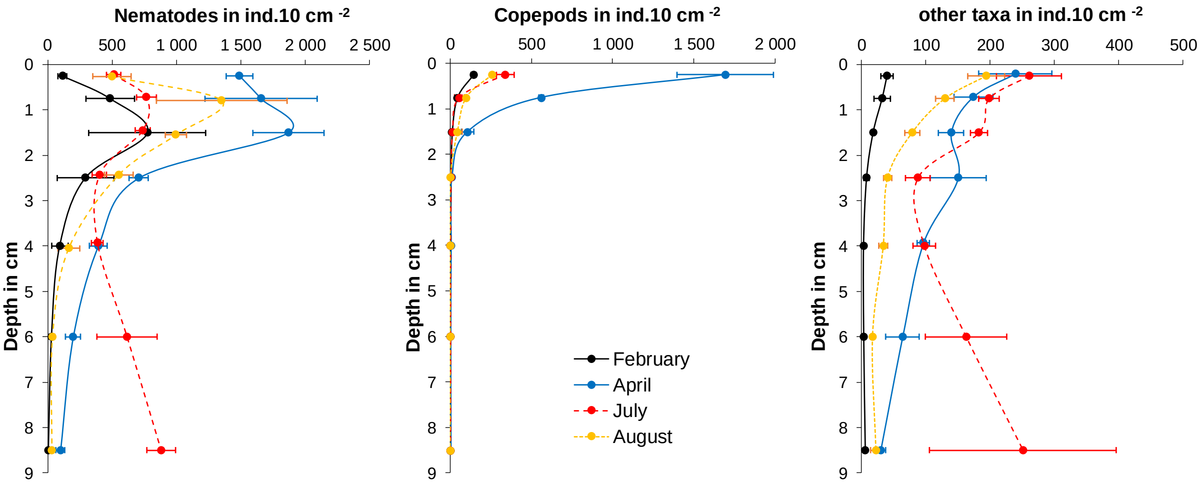

Figure 6: Vertical distribution of meiofauna (nematodes, copepods and other taxa) at the MESURHO station in February, April, July and August 2010. Values are means ± SEM (n=3 cores). Note that some symbols were slightly shifted vertically relative to each other for visibility.

The vertical distribution of the meiofauna in July differed from the general pattern with high abundances in the deep layers similar to those recorded in the very upper layers of the other dates (two-way ANOVA, $p < 0.001$, Supplementary material, Table S5). The vertical profiles of copepods seem to fit the pattern of oxygen penetration depth (Fig. 2), but this clearly does not apply to nematodes and foraminiferans, which displayed the highest abundances in deep sediment layers (5 to 10 cm depth, Supplementary material, Table S2). These changes in the vertical distribution of the main meiofaunal taxa occurred just a couple of days after the flood of the Rhône tributaries and the sudden increase in TSM (Fig. 1). The drop in meiofaunal total abundance and the presence of a high density of nematodes in the deep layers after this high-discharge event can be explained by the burial of the meiobenthic community as observed experimentally with the simulated deposition of dredged material (Schratzberger et al., 2004). As so the present results corroborate the observation of Pelletier (1999) that high-discharge events severely affect the meiofauna with a reduction of its abundance. Among the "other taxa" the clear dominance of foraminifera from genus *Leptohalysis* was noted in July. This foraminiferan is considered as an opportunistic taxon resistant to high turbidity, large inputs of terrestrially-derived OM, and low oxygen penetration in the sediment (Mojtahid et al., 2009; Scott et al., 2005). An opportunistic strategy allows *Leptohalysis* to proliferate in the Rhône prodelta in just a few days after a flood (Goineau et al., 2012).

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

3.6. Linking meiofaunal composition and sediment properties

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

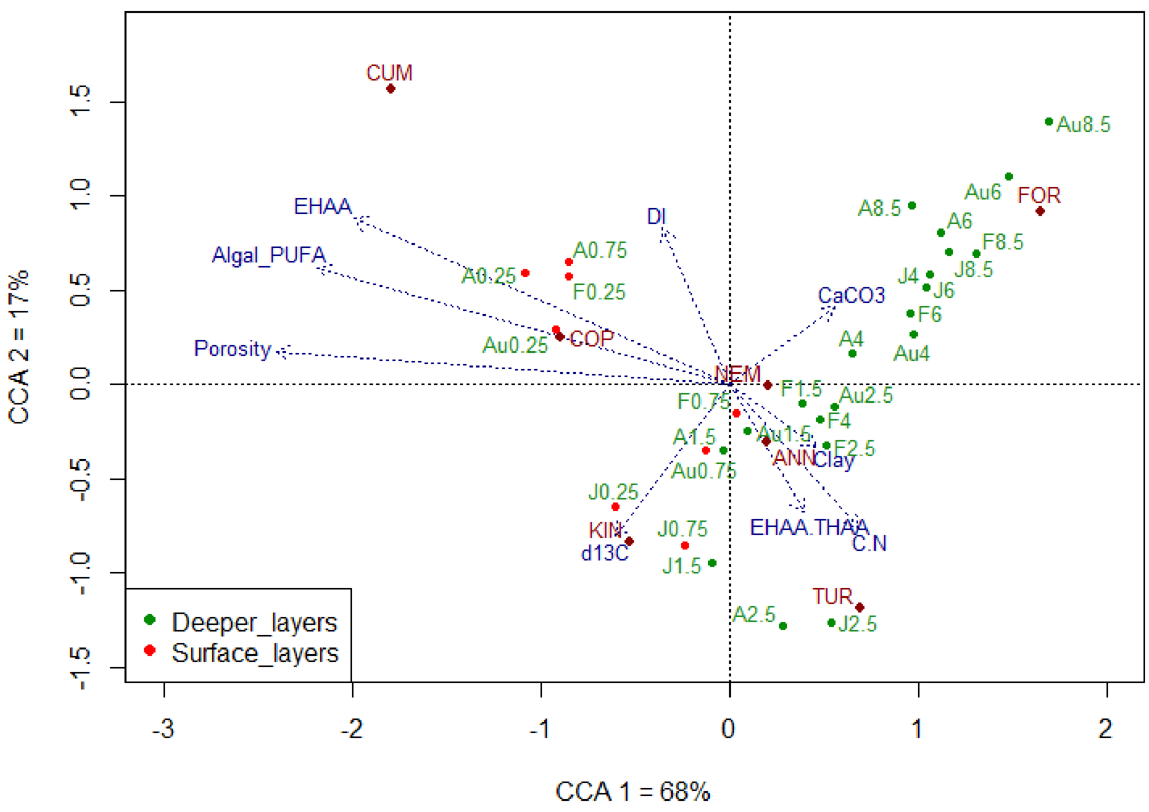

Figure 7: Canonical correspondence analysis (CCA) triplot showing ordination of meiofaunal taxa at the MESURHO site in February, April, July and August 2010 with environmental variables as arrows and samples as dots.

Nematodes (NEM), copepods (COP), kinorhynchs (KIN), annelids (ANN), turbellarians (TUR), cumaceans (CUM), and foraminiferans (FOR). Environmental variables are C/N = molecular carbon to nitrogen ratio, δ^{13}C = bulk stable isotope value, EHAA: normalised concentration in enzymatically hydrolysable amino acids, EHAA/THAA: enzymatically hydrolysable amino acids to total hydrolysable amino acid ratio, DI= degradation index, algal PUFA = normalised concentration in algal polyunsaturated fatty acids, clay= proportion of clay, $CaCO_3$ = calcium carbonate percentage, and porosity.

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

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

The constrained ordination also displayed how the meiofaunal taxa were structured with respect to their environmental constraints and agreed well with the known ecological niches of the recorded taxa. Many cumaceans and harpacticoid copepods rely on planktonic diatoms sinking on the seafloor (De Troch et al., 2005; Giere, 2009; Higgins and Thiel, 1988). In good consistency with their feeding habits, cumaceans and copepods were related to inputs of fatty acids produced by phytoplankton and higher level of bioavailable amino acids found on the top of the cores. Kinorhynchs belong to another group with a known preference for the upper (0-3 cm) oxygenated surface layers (Giere, 2009). Shallow water forms feed mainly on diatoms, but they are also linked to organically enriched sediments (Higgins and Thiel, 1988) as those found near river mouths (Guidi-Guilvard and Buscail, 1995). As expected, kinorhynchs were found in the surface sediments, but they displayed high relative frequencies (~13%) in the flood deposit that recovered the seafloor in July. While kinorhynch density in the top layers remained constant from April to August, copepod and cumacean densities dropped remarkably after the flood (Supplementary material, Table S2). This shows that crustaceans and kinorhynchs respond differently to river regime. In a mesocosm study, Rudnick (1989) found that copepods and kinorhynchs belong to two distinct feeding groups; the first group consuming fresh OM, while the second one could use older detrital matter. However, since the sampling only occurred a few days after the flood, it seems unlikely that the nature of the available OM could be the factor affecting meiofaunal community in July. Kinorhynchs can perform vertical movements in the sediment (Shimanaga et al., 2000). A higher capacity to migrate upward and colonise the newly flood deposit could explain the apparent resilience of kinorhynchs to the physical perturbation induced by the high-discharge event. Nematodes and annelids were the taxa whose occurrence and variability in density were the less explained by the CCA. Free-living nematodes, the metazoans with the greatest species richness in the sediments, occupy various ecological niches with different trophic requirements and sediment preferences (Giere, 2009; Moens et al., 2013), which may explain their wide vertical distribution. The ordination showed anyway their preference for subsurface and deeper sediment layers. Like nematodes, meiobenthic annelids are euryoecious, their preferences relate to sediment structure and organic content (Giere, 2009; Villora-Moreno, 1997). In the present study, they were related to ascending EHAA/THAA and C/N ratios. Foraminiferans were associated with deeper sediment layers and $CaCO_3$. Most foraminiferans are versatile for microhabitat selection, food supply and oxygen availability. Mojtahid et al. (2010) investigated microhabitat preferences of living foraminiferans in front of the Rhône River mouth. They found two different assemblages: infaunal species with maximum densities in anoxic layers were dominant close to the river mouth, while species living predominantly in the top surface layer dominated in areas less influenced by fluvial inputs. They postulated that the higher tolerance of infaunal species for degraded terrestrial OM explains their dominance in the prodelta area. This is consistent with the CCA ordination showing that foraminiferans were related to rather low $\delta^{13}C$ (meaning higher contribution of terrestrial OM). Finally, turbellarians, a group with predatory habits or feeding on diatoms, only occurred in two samples (layers 2-3 cm in April and July).

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

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

4. Conclusions

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

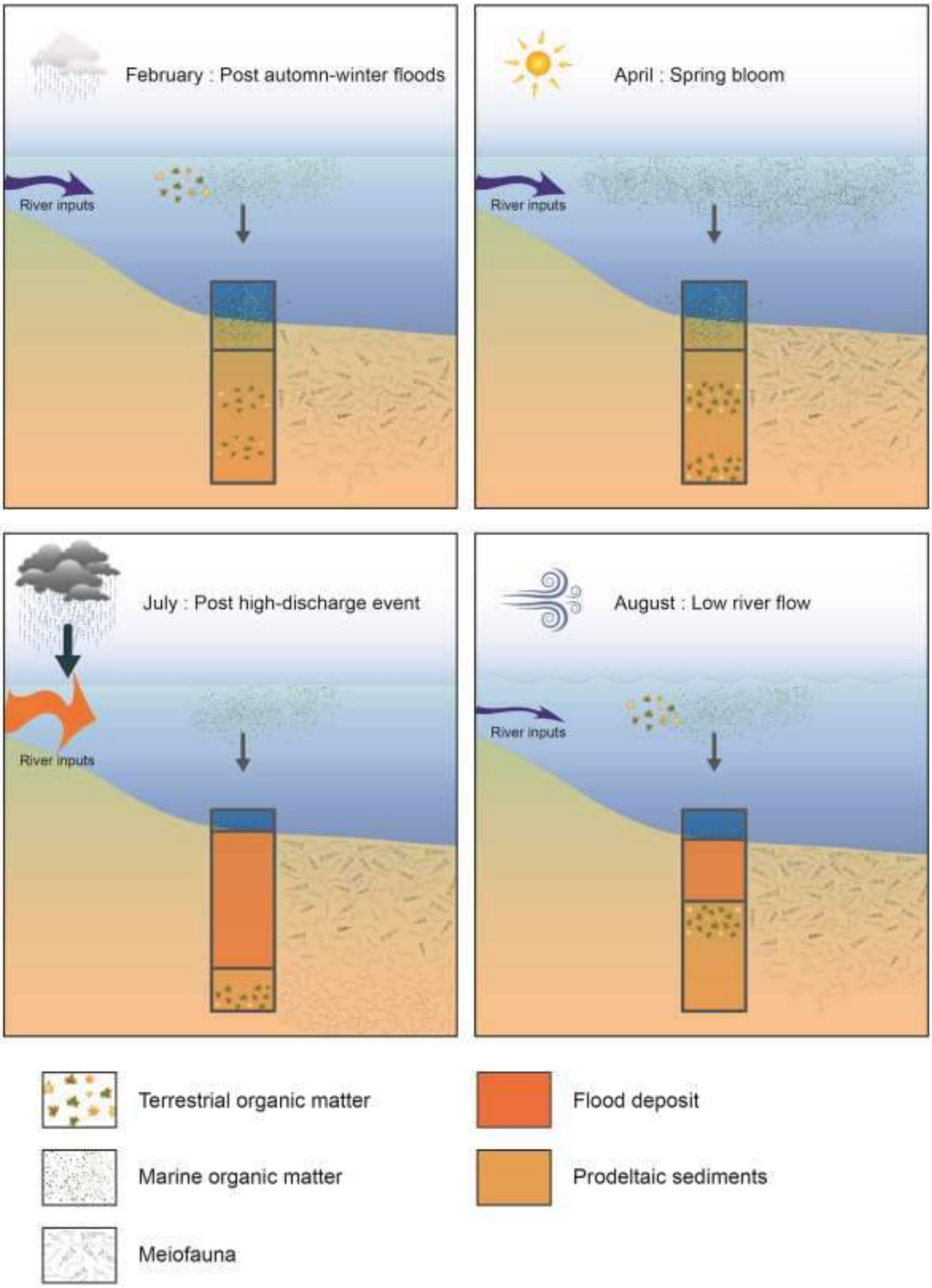

Figure 8: Synthetic scheme of the processes influencing the dynamic of organic matter and meiofaunal community composition during the four investigated periods in the Rhône prodelta.

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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)
$\delta^{13}C$	Source	Marine OM (−20.1±0.8‰) and Rhône River inputs (−27.1 ± 0.6‰)	Harmelin-Vivien et al. (2008) and Higueras 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 $C_{20:5\omega3}$ specific of diatoms	Dunstan et al. (1994)
MUFA	Source	Mixed origin with $C_{16:1\omega7}$ common in diatoms and bacteria	Bianchi and Canuel (2011), Dunstan et al. (1994)
BAFA	Source	Bacterial sources	Bianchi and Canuel (2011)

The degradation index (DI), reactivity index (RI) and enzymatically hydrolysable amino acids to total hydrolysable amino acids ratio (EHAA/THAA) are inferred from the amino acid composition. Fatty acid biomarkers are grouped as follows: mid-chain even-number saturated fatty acids with less than 20 carbons (MC-SAFAs), long-chain saturated fatty acids with 24 carbon or more (LC-SAFA), polyunsaturated fatty acids with 18 carbons ($C_{18:2\omega6}$ and $C_{18:3\omega3}$, Terr PUFA), the remaining PUFA attributed to microalgae (Algal PUFA), the monounsaturated fatty acids (MUFA) and the straight and branched odd-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 multiplied by its percentage of the total fatty acid composition.

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

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

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

Marginal effects						**Conditional effects**					
Rank	**Variable**	**AIC**	**F ratio**	**Pr(>F)**		**Rank**	**Variable**	**AIC**	**F ratio**	**Pr(>F)**	
1	**Porosity**	79.935	7.267	0.005	**	1	**Porosity**	79.935	7.267	0.005	**
2	**Algal PUFA**	81.865	5.0518	0.005	**	2	**$\delta^{13}C$**	78.509	3.2544	0.015	*
3	**EHAA**	81.042	5.9774	0.015	**	3	**DI**	77.785	2.4517	0.045	*
4	C/N	85.621	1.1536	0.270		-	EHAA	78.170	1.3657	0.180	
5	$\delta^{13}C$	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	$CaCO_3$	86.252	0.5482	0.655		-	$CaCO_3$	79.301	0.4013	0.820	
9	Clay	86.343	0.4626	0.715		-	C/N	79.419	0.303	0.925	