Relationship between bacterial compartment and particulate organic matter (POM) in coastal systems: an assessment using fatty acids and stable isotopes

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Abstract

Particulate organic matter (POM) in coastal systems is a mixture of different organic matter (OM) sources originating from land and sea. Among sources, bacterial biomass plays a large role in OM processing and carbon recycling in the ocean and is often neglected as a source in common approaches. The present study proposes to use elemental and isotopic ratio of carbon and nitrogen (C:N, $\delta^{13}C$, $\delta^{15}N$) and fatty acids to investigate the relationship between bacteria and surface water POM composition of three systems with different characteristics (two marine and one estuarine) over an annual cycle. Overall, our results highlight a positive relationship between bacterial contribution and continental degraded or undergoing degradation POM for all the studied systems and an inverse relationship with pelagic primary producers. At multisystem scale, high bacterial contribution is linked to high proportion of refractory terrestrial material characterizing estuarine stations whereas in marine systems, the occurrence of bacteria is mainly linked to river POM. Over the annual cycle, bacterial markers are more abundant during the winter period characterized by larger river and/or benthic POM contribution. This seasonal pattern is mainly driven by changes in river flows and resuspension. This study highlights the importance of bacterial compartment as a component of coastal and estuarine POM. Even though these results remains semi-quantitative, similar studies in other types of systems can help to understand microbial role in OM dynamic and to better estimate bacterial source in carbon budgets and food web studies.

Keywords: POM dynamic; bacteria; $\delta^{13}C$; $\delta^{15}N$; fatty acids; mixing models; French littoral.

1. Introduction

Coastal systems are amongst earth's most productive systems (Duarte & Cebrián, 1996; Gattuso et al., 1998) promoting an intense biological and biogeochemical activity (Smith and Hollibaugh, 1993) responsible for production and exchange of matter between land and sea. Coastal systems generate 12% of oceanic primary production (Dunne et al., 2007) and a non-negligible part of matter inputs originate from rivers as dissolved or particulate material (Ludwig et al., 1996). In addition, organic matter (OM) fluxes are largely induced or regulated by living organisms (i.e. primary and secondary production, remineralization, etc.). Within these systems, suspended particulate organic matter (POM) is a result of multiple inputs from adjacent compartments. POM is composed of numerous sources of organic carbon including phytoplankton, bacteria, benthic macro- and micro- primary producers, terrestrial OM from river inputs (Liénart et al., 2017; Tesi et al., 2007a; Volkman and Tanoue, 2002). However, the diversity of sources and the numerous process acting on POM composition and dynamics make difficult to characterize and quantify the contribution of each source to the POM pool. In addition, within these sources, bacterial compartment is often neglected.

Heterotrophic prokaryotes (i.e. bacteria) play an important role in OM processing in the ocean (Azam et al., 1983). Particulate organic carbon (POC) processing by these organisms in epipelagic zone leads to the recycling of c.a. 90% of the OM produced by photosynthesis (Wakeham et al., 1984) that is converted in new biomass, degraded into smaller particles (external enzymatic degradation, e.g. Smith et al., 1992) or turned into dissolved organic and inorganic carbon (Wakeham and Lee, 1993). In the water column, bacteria are present as free cells or attached to particles, which they use as a growth substrate (Kiørboe et al., 2002). Bacterial biomass attached to particles has been estimated as contributing up to 14% of total bacterial production (i.e. free cells and attached) in oligo- and mesotrophic pelagic systems and reaching 30% in eutrophic and estuarine systems characterized by high turbidity (Simon et al., 2002 and references therein). In a general way, bacterial contribution to the OM pool largely depends on environmental factors and on particle concentration (Simon et al., 2002), origin and nature (i.e. lability). The substantial role of microbial processes in biogeochemical cycles and energy transfer within food webs makes bacteria a central component of the ecosystem functioning, although its action may differ depending on the studied systems. For instance, in the Baltic Sea, a shift toward more bacteria-based food webs may reduce pelagic productivity at higher trophic levels (Berglund et al., 2007). In contrast, bacterial compartment is an important link between mesozooplankton and degraded particles by being an interesting food source for pelagic and benthic organisms (i.e. David et al., 2016 in the Gironde Estuary, France; Meziane et al., 2002 in subtropical intertidal flat, Okinawa, Japan).

Investigating bacteria in the ocean has always been methodologically challenging. Single cells are difficult to isolate due to their small size but also due to the complex mixture of particles in seawater (e.g. phytoplanctonic cells, detritus; Kemp et al., 1993). The most common approach to estimate the contribution of a given organic matter source in carbon budgets or in a POM pool is to use stable isotopes (SI) ratio of carbon and nitrogen ($\delta^{13}C$, $\delta^{15}N$), C:N elemental ratio or other biomarkers such as fatty acids (FA) as OM tracers (e.g. Connelly et al., 2016; Dubois et al., 2014; He et al., 2014; Lowe et al., 2014). Thanks to the distinct signatures of the sources (e.g. marine *versus* continental, different primary producers), elemental and isotopic ratios have been used in numerous studies characterizing the origin and composition of POM in coastal systems and even to quantify the contribution of each source to the POM pool by using mixing models (e.g. Berto et al., 2013; Cresson et al., 2012; Liénart et al., 2017). However, classical isotopes studies (i.e. on 'bulk' POM from field samples) cannot attempt estimating the contribution of bacterial biomass to the POM pool: isotopic signature of both bacteria and its substrate is supposed to be identical.

Among other, FAs appear to be a relevant proxy to reveal the bacterial biomass. These compounds are the main structural components of cell membranes, a high source of metabolic energy and are, in many circumstances, conservatively preserved in cells contrarily to other molecules (e.g. proteins) (Dalsgaard et al., 2003). Moreover, FAs biosynthesis varies depending on the targeted organisms (e.g. primary producers, consumers, bacteria) making single FA a suitable tool (trophic marker, concept of FATM) for the identification of taxonomic groups (Dalsgaard et al., 2003) and to trace its transfer along food webs (e.g. Hall et al., 2006; Kelly and Scheibling, 2012). Branched FA (BrFA) are typically synthetized by bacteria (Dalsgaard et al., 2003; Rajendran et al., 1993; Volkman et al., 1980) and more specifically, C_{15} and C_{17} iso- and anteiso- (15:0iso, 15:0anteiso,17:0iso, 17:0anteiso) are described as markers of bacterioplankton (Budge and Parrish, 1998; Desvilettes et al., 1997; Hall et al., 2010). Among others, FAs biomarkers have been used to discriminate phytoplankton from macroalgae in marine sediments (Hu et al., 2006; Meziane et al., 2006, 1997), to distinguish autochthonous (i.e. primary production) from allochthonous (i.e. terrestrial OM) sources of POM in coastal waters (Lowe et al., 2014; Xu and Jaffé, 2007) and to investigate bacterial contribution as food source (Meziane et al., 2002).

There is an increasing interest in characterizing POM pool composition but only few studies discussed and tried to estimate bacterial biomass contribution to pelagic POM (e.g. Berto et al., 2013; Bourgoin and Tremblay, 2010; Savoye et al., 2012). The present study proposes to estimate the relationship between bacterial compartment and POM in surface water of five stations belonging to three coastal systems with different biological, biogeochemical and geomorphological characteristics. It aims evaluating the link between bacteria and the different POM sources 1) at multisystem scale, considering system types and 2) over the seasonal cycle, at local scale, by using two complementary approaches: fatty acids biomarkers, which is the core of this study, and elemental and isotopic ratios of carbon and nitrogen (as in Liénart et al., 2017). Spatial and temporal variability of bacterial contribution are expected to be linked with those of OM sources and more particularly, bacterial biomass is expected to be high in systems characterized by an intense biogeochemical activity (homogeneous POM composition due to heterotrophic processing, i.e. Middelburg and Herman, 2007) or with higher turbidity (more particles as substrate, i.e. Simon et al., 2002). Bacterial contribution is also expected to increase with more degraded material or OM undergoing degradation processes (Abril et al., 2002), during winter or just after inputs of fresh organic material.

2. Materials and methods

2.1. Study systems and sampling

Five stations belonging to three systems (Fig. 1) characterized by different geomorphological features and biogeochemical properties (salinity ranges, turbidity, trophic status, etc.) were sampled for surface water (c.a. 1m depth water) for the years 2014-2015. Two systems are located on the Atlantic coast: the Gironde estuary, a macrotidal, turbid and eutrophic estuary, and Arcachon lagoon, a mesotidal, mesotrophic semi-enclosed lagoon. The third system is located on the Mediterranean coast: the oligotrophic open bay of Banyuls-sur-mer. The Gironde estuary was monthly sampled at high (HT) and low (LT) tides at three stations (from upstream to downstream: pk30, pk52, pk86) along the salinity gradient (c.a. 0-30) from March 2014 to March 2015. As high and low tide sampling of a single station correspond to the sampling of different water masses, each combination tide x station was considered as independent to each other, just like if six different stations were sampled. Arcachon lagoon (station Eyrac) was bi-monthly sampled at high tide from February 2014 to February 2015. The bay of Banyuls (station Sola) was bi-monthly sampled from December 2014 to August 2015. For a better understanding, system's name are used to describe our study sites.

Samples for POM surface water FA analysis were collected at the same stations and dates as those for which sixteen physical, biogeochemical and biological parameters (including POC and PON concentrations, $\delta^{13}C$ and $\delta^{15}N$ used in the present study) are measured by the SOMLIT coastal monitoring program (Service d'Observation en Milieu LITtoral - http://somlit. epoc.u-bordeaux1.fr/fr/).

Water was sampled using a Niskin bottle and stored in the dark in a pre-cleaned container. Back to the laboratory, water samples were gently homogenised, then filtrated for FA analysis through pre-combusted (4 h - 450 °C) and pre-weighted GF/F filters (47 mmØ) using a glass filtrating system. Three filters were sampled for each date and stored frozen (-80°C) until the analysis. The range of filtered volumes varied depending on the ecosystem from 40mL to 1.5L for the Gironde estuary, from 1 to 3.5L for Arcachon lagoon and from 1 to 6L for the bay of Banyuls.

2.2. Fatty acid extraction and analysis

The method used for the Fatty Acids (FA) extraction follows largely the Bligh and Dyer method (1959) as adjusted in Meziane et al., (2006). To quantify FA concentrations, a known volume of a commercial internal standard (C23:0, concentration of 5 mg/mL) was introduced in each sample. For POM and SOM analyses, half-filters were soaked in a distilled water-chloroform-methanol solution (1:1:2, v:v:v) and sonicated during 20 minutes for the FAs extraction. Samples were thereafter completed by a distilled water-chloroform solution (1:1, v:v) and centrifuged (3 000 rpm, 5 minutes). Lipid phases were transferred in others tubes, completed by a distilled water-chloroform solution (1:1, v:v) and sonicated again during 20 minutes in order to maximize the extraction. Then, samples were evaporated under a dinitrogen (N_2) flux, diluted a second time in a mixture of methanol and sodium hydroxide (2:1, v:v; [NaOH] = 2 $mol.L^{-1}$) and heated at 90°C during 90 minutes for FAs saponification. Finally, FAs were converted into FA methyl esters after (FAME) for ten minutes at 90°C using a methanolic boron trifluoride solution (BF_3-CH_3OH 14%, 1 mL). At the end of the reaction, the chloroform phase containing FAMEs was retrieved and stored at – 20°C.

FAMEs were analyzed by both gas chromatography (Varian 450-GC-FID) for individual FAMEs quantification and gas chromatography mass spectrometry (Varian 220-MS-ion trap) for FAMEs identification. FA nomenclature is defined as X:YωZ (correcting the corresponding FAME for the added methyl group) where X is the number of carbon atoms, Y the number of double bonds and Z the position of the last double bond from the methyl group. The C23:0 standard allowed converting each FA methyl esters area into a quantity thanks to the following equation:

$$C_{FAME} = \left(\frac{A_{FAME}}{A_{C23}} \times \frac{C_{23}}{M_f} \right)$$

Where C_{FAME} is the FA methyl ester concentration (µg/g), A_{FAME} is the FA peak area, A_{C23} is the C23:0 peak area, C_{23} is the C23:0 quantity (µg) added in each sample and M_f is the mass of matter deposited on the half-filter analyzed.

2.3. Stable isotopes analysis

Within the scope of the SOMLIT coastal monitoring program, surface water was sampled, processed and analysed for elemental and isotopic ratios of C and N ($\delta^{13}C$, $\delta^{15}N$, C:N) following standardized protocols available on the SOMLIT website (http://somlit.epoc.u-bordeaux1. fr/fr/spip.php?rubrique13). Existing datasets of the targeted parameters used in this study were retrieved from the SOMLIT database (http://somlit.epoc.u-bordeaux1.fr). More information concerning stable isotope analysis are also available in Liénart et al., (2017).

2.4. Numerical analysis

Analyses were performed with the free software R (http://cran.r-project.org, R development core team, 2014).

2.4.1. Biomarker data pre-treatment

For each sampling date and identified FA, an average value of the triplicates profiles was computed. This value was used for the statistical analysis. Single FAs with an average of contribution to total FAs below 1% were not considered. Functional groups of FA were computed: Saturated (SFA), monounsaturated (MUFA), polyunsaturated (PUFA) and Branched (BrFA).

FA groups proportions and elemental and isotopic ratios were compared between stations using a non-parametric Kruskal-Wallis test (KW) (i.e. parametric conditions not met) followed by a pairwise multiple group comparison test (Nemenyi test, 'PMCMR' package).

2.4.2. Organic matter sources and mixing models

Composition of POM was assessed following the method developed and discussed by Savoye et al., (2012) and Liénart et al., (2017). Possible organic matter sources are from two main origins: autochthonous (i.e. in situ pelagic and benthic primary production) and allochtonous (i.e. originating from continent, carried by rivers, run-off or artificial outlets). In literature, commonly used sources in POM mixing models are marine phytoplankton, benthic macrophytes, microphytobenthos and anthropogenic POM (e.g. Berto et al. 2013, Cresson et al. 2012, Dubois et al. 2012, Liénart et al. 2016), but not all sources contribute to the POM pool in all types of coastal systems.

For each system, potential sources of organic matter contributing to POM composition were carefully identified and additionally sampled (for each site, monthly over an annual cycle, see Liénart et al. 2017 for sampling strategy) considering system specificities based on previous studies and knowledge of local experts. For each of the selected sources, elemental and isotopic signatures were either measured directly or estimated when no direct measurement was possible (e.g. phytoplankton, see Liénart et al. 2017) over an annual cycle, for each station independently. Prior to POM composition calculation, temporal variability of elemental and isotopic signature of each source was considered for each station (see Table 1), if needed and when possible, using 1) empirical multi-regressive models or 2) average ± standard deviation. The range of values of each parameter was associated to specific signatures for each source. This allowed the discrimination of the different sources. Almost all coastal POM values were within the limits of the signature of possible sources for all sites (Fig. S1). Source signatures were estimated for each sampling date and station (cf. averages and equations in Liénart et al., 2017).

To avoid bias and to minimize the uncertainty associated to the mixing-model outputs, only relevant sources were used as end-members in each studied system, based on previous studies and mathematical considerations (e.g. Fry 2013, Phillips and Gregg 2003). Mixing models based on a Bayesian approach (SIAR package; trophic enrichment factor = 0, siarsolomcmcv4; Parnell et al., 2010) were run for each sampling date and each station by using isotopic ($\delta^{13}C$, $\delta^{15}N$) and elemental (N:C ratio) values of sources and bulk POM for the Arcachon lagoon and the bay of Banyuls. The absolute uncertainty associated to the mixing-model outputs was usually close to 10%. For the Gironde estuary, the $\delta^{15}N$ and C:N ratio does not allow the discrimination of the sources in this specific system. Thus, $\delta^{13}C$ and the ratio of POC to suspended particulate matter were used to calculate the relative proportion of each sources at each sampling date for each station following the approach developed by Savoye et al., (2012) for this specific system.

2.4.3. Multivariate analysis

Spatial variability – Principal Component Analysis (PCA, dudi.pca() function, ade4 package) were performed for the eight combinations stations x tides i) on the overall FA dataset, ii) on POM composition (proportions) calculated by mixing models. Mixing models outputs were computed in diagrams as mean annual value of each source for a given station.

Seasonal variability – First, to define seasonal periods over the annual cycle, a constraint agglomerative hierarchical classification method (CAHC, chclust() function, rioja package), which preserves chronological order of the data, was performed based on an euclidian association matrix, on the overall FA dataset for each station separately. Second, PCAs were performed (s.class() function, ade4 package) for each stations independently on the overall FA dataset in order to explain seasonal variability observed between these periods. Finally, mixing model outputs were computed as diagrams of POM composition for each period previously identified by the CAHC analysis.

Bacterial contribution – The link between bacterial FA markers and POM composition (% sources from mixing models or FA markers of specific groups) was investigated with linear regressions.

3. Results

3.1. Fatty acids

Fifty-eight individual fatty acids were identified over all POM samples: 38 for the estuarine POM, 41 for Arcachon lagoon POM and 48 for the bay of Banyuls POM (Supplementary Table 1). Most of the identified FAs were ≤ C_{20} chains, representing ca. 95% of the total fatty acids (TFA). For all the stations, each individual contribution of 5 FAs exceeded 10% of TFA: 14:0, 16:0, 16:1ω7, 18:0 and 19:1ω9. The combination of these 5 FAs represented in average 61 to 67% of the TFA depending on the station. Secondary FAs identified (i.e. FAs with individual contribution ranging from 1 to 10% of TFA) differ in terms of presence and contribution between stations. Nevertheless, the essential fatty acids (EFA) 20:5ω3 and 22:6ω3 as well as 15:0, 15:0anteiso, 17:0anteiso, 16:1ω5, 16:1ω9, 18:1ω7, 18:2ω6, 18:3ω3, 18:4ω3 were generally identified at each station.

Over the studied stations and tides, total saturated FA (SFA) contributed in average to 53 to 61% of the TFA. Total monounsaturated FA (MUFA) showed relatively constant proportion (19 to 24%) whereas total polyunsaturated FA (PUFA) and branched FA (BrFA) exhibited variable contributions (respectively ca. 9 to 20% and 2.5 to 10%) of the TFA. No significant differences in SFA contribution were found between stations except between the bay of Banyuls and Arcahon lagoon (KW, posthoc Nemenyi test, $p<0.05$; Fig. 2, A). MUFA contribution was not significantly different between the studied stations (Fig. 2, A). PUFA contribution was significantly higher (KW, posthoc Nemenyi test, $p<0.05$) for Arcachon lagoon than for the upstream and middle estuarine stations at high and low tides (pk30HT, pk30LT, pk52HT, pk52LT) as well as with the bay of Banyuls (Fig. 2, A). BrFA contribution was significantly lower (KW, posthoc Nemenyi test, $p<0.01$) for Arcachoon lagoon and the estuarine stations at high and low tides and for the bay of Banyuls and the upper and middle estuarine stations at high and low tides (Fig. 2, A). It clearly appeared that 1) there was a gradient of PUFA and BrFA along the Gironde estuary and 2) the bay of Banyuls exhibited intermediate values compared to the estuarine stations on the one hand and Arcachon lagoon on the other hand.

3.2. Elemental and isotopic ratios of POM and organic matter sources

C:N ratio of POM was in average 7.8 mol.mol^{-1} with values ranging from ca. 5 to 10 mol.mol^{-1} (Fig. 2, B), with higher average values for the estuarine stations (ca. 8 mol.mol^{-1}) than for the marine stations (ca. 7.3 mol.mol^{-1}). POM $\delta^{15}N$ was in average ca. 5‰ with values ranging from ca. 1.5 (bay of Banuyls) to more than 8 in the Gironde estuary (Fig. 2, B); the Mediterranean station of the bay of Banyuls exhibited the lowest average value (ca. 4.2‰). No significant differences were found between the stations for these two parameters. POM $\delta^{13}C$ values ranged between -26‰ and -19‰. Significant differences (KW, posthoc Nemenyi test, $p<0.05$) were found between Arcachon lagoon and the estuarine stations except pk86HT, and between the bay of Banyuls and pk30 and pk52 at both tides (Fig. 2, B). It clearly appeared that 1) there was an overall gradient of isotopic ratios along the Gironde estuary and 2) the bay of Banyuls exhibited intermediate values compared to the estuarine stations on the one hand and Arcachon lagoon on the other hand.

In each studied system, elemental and/or isotopic ratios enable discriminating each organic matter source and allow the use of mixing models in order to quantify the proportion of each source within the POM (Table 1; Savoye et al., 2012; Liénart et al., 2017; see 2.4.2).

3.3. POM composition

In the marine systems, POM composition was highly dominated by phytoplankton: 79% for Arcachon lagoon and 70% for the bay of Banyuls (Fig. 3). The contribution of the other sources varied depending on the station: river POM ranged from 8% in Arcachon lagoon to 11% in bay of Banyuls and among other primary producers, diazotrophs represented 19% of the POM of the bay of Banyuls whereas benthic primary producers in Arcachon lagoon were about 7% and 6% for microphytobenthos and macrophytes contribution respectively (Fig. 3).The Gironde estuary POM was mainly composed by refractory terrestrial material, from 66% to 92% depending on the station and tide (Fig. 3). Labile terrestrial POM contributed from 2 to 10% of the POM and phytoplankton from 2% for the upper estuary up to 30% in the downstream estuary at high tide.

4. Discussion

4.1. A continent-ocean gradient

The spatial variability of FA profiles and POM composition at the studied stations is summarized in two principal component analyses (PCA) (Fig. 4 and 5). Both clearly show a continent-ocean gradient of POM origin and bacterial contribution at multisystem scale, which opposes marine to estuarine stations. This gradient is also seen at local scale within the Gironde estuary from upstream to downstream stations.

At a multisystem scale, the estuarine stations of the Gironde (pk86, pk52 and pk30) are opposed to the marine stations of the bay of Banyuls and Arcachon lagoon. This gradient is observed with both fatty acids (PCA Fig. 4, axis 1) and POM composition data (PCA Fig. 5, axis 1). In the estuarine stations, POM is characterized by a dominance of refractory terrestrial material (i.e. 83% average for all stations and tides, Fig. 5), which is a typical feature of the Gironde estuary (Etcheber et al., 2007; Savoye et al., 2012). FA profiles show larger contribution of SFA (12:0, 13:0, 15:0, 18:0, Fig. 4) and lower of PUFA, which is typical of degraded POM as PUFA and MUFA are rapidly degraded in aquatic systems (Meyers, 2003; Saliot et al., 2001) compare to SFA (Meyers and Eadie, 1993). The relative proportions of these groups of FA in a POM pool is thus used as indicator of its freshness or degradation level (Canuel, 2001; Mortillaro et al., 2011). Compared to marine systems, POM in the estuary is also associated to a higher bacterial biomass reflected by a larger contribution of BrFA (Fig. 4; Fig. 2; typical markers: 15:0iso, 15:0anteiso, 16:0iso, 17:0anteiso, Rajendran et al., 1993; Volkman et al., 1980). The Gironde estuary is a 'tidal-dominated' estuary (Middelburg and Herman, 2007) characterized by high turbidity and long residence time of particles which induce low primary production and intense remineralisation (Abril et al., 2002, 1999; Etcheber et al., 2007) and leads to the typical observed POM profiles. Increasing contribution of bacteria and related FA markers with larger amounts of detrital / refractory material have been illustrated by other authors (i.e. Lowe et al., 2014; Mortillaro et al., 2012). By opposition, phytoplankton dominates POM composition in marine systems from 70% at the bay of Banyuls to 79% in Arcachon lagoon (Fig. 5). In open ocean but also in coastal marine systems, phytoplankton is the major source of POM (Bode et al., 2006; Cresson et al., 2012; Lebreton et al., 2016; Liénart et al., 2017, 2016; Lowe et al., 2014) which relative contribution varies over space and time (Liénart et al., 2017). In the bay of Banyuls and Arcachon lagoon, POM is likely 'fresh' (i.e. alive phytoplanktonic cells), characterized by a higher contribution of 16:1ω7 and the PUFAs 16:4ω1, 18:2ω6, 18:3ω3, 18:4ω3, 20:5ω3 and 22:6ω3 (Fig. 4). Primary producers are organisms capable to *de novo* produce PUFAs, ω3 and ω6 with long carbon chain such as the EFA 20:5ω3 and 22:6ω3 (e.g. Cook 1996; Sargent and Henderson, 1995), or to add double bonds and extend carbon chains from SFA or MUFA (Dalsgaard et al., 2003). The association of these FAs in the POM pool emphasize the dominance of primary producers in the two marine systems as similarly found by Lowe et al., (2014) and Mortillaro et al., (2012).

Within marine stations, the contrast between Arcachon lagoon and the bay of Banyuls is observed with both FA (PCA Fig. 4, axis 2) and POM composition (PCA Fig. 5, axis 2) even though more precisely described by FA profiles. At Arcachon lagoon, higher contributions of 16:1ω7, 16:4ω1 and 18:4ω3 (Fig. 4) show the presence of some macroalgae and diatoms (Dalsgaard et al., 2003; Kelly and Scheibling, 2012 and references therein) and 18:2ω6, 18:3ω3, 18:4ω3 and 22:6ω3 (Fig. 4) of macrophytes and associated epiphytes at different degradation stages. These FA reflects benthic OM influence, a similar pattern also identified by Dubois et al., (2014) in this system. Typically, in shallow systems, benthic contribution to the surface water POM can be high due to strong benthic-pelagic coupling processes (Malet et al., 2008; Modéran et al., 2012). In Arcachon lagoon, a shallow (ca. 8m at Eyrac) semi-enclosed lagoon under tidal influence, macrophytes and benthic microalgae that are widely developed and significantly fuel the POM pool (e.g. Dubois et al., 2012; Schaal et al., 2008, Fig. 5) due to resuspension processes (e.g. Dubois et al., 2012; Liénart et al., 2018). By contrast, the bay of Banyuls shows a POM composition dominated by pelagic primary producers (i.e. phytoplankton and diazotrophs: 89% total, Fig. 5) even though FA markers of phytoplankton are less represented than in Arcachon lagoon (Fig. 4). The oligotrophic Mediterranean Sea is characterized by the presence of atmospheric N_2-fixing organisms in phytoplankton communities (i.e. diazotrophs, Kerhervé et al., 2001; Zeev et al., 2008) that are able to cope with N limitation and have a non-negligible contribution to the POM pool (19%, Fig. 5). However, as primary producers, N_2-fixing organisms have FA profiles identical to the 'classical' phytoplankton ones (i.e. C14, C16, 18:1ω9) (Carpenter et al., 1997; Vargas et al., 1998) leading to difficulties in identifying separate FA markers for this source. In comparison to Arcachon lagoon, the POM of the bay of Banyuls has lower proportions of PUFA (ca. 12 *vs* 21%, Fig. 2) and higher contributions of SFA (ca. 61 *vs* 53%, Fig. 2) and BrFA (3.6 *vs* 2.5%, Fig. 2). SFA indicate degraded material and, in marine environments, of POM from terrestrial origin (e.g. Budge et al., 2001). The bay of Banyuls is an open bay with water masses coming from the open ocean influencing on its POM composition. In the Gulf of Lion, marine currents are mainly coming from the east and carry particles from the surrounding rivers (Higueras et al., 2014) and more particularly material from the Rhône River that can be detected far from the river mouth (Tesi et al., 2007b). It explains the rather large inputs of continental (likely degraded) material at this station (11%, Fig. 5) also reflected by the presence of some specific FAs (e.g. 24:0, Fig. 4), and is consistent with the larger bacterial contribution compare to Arcachon lagoon.

At local scale, POM composition of the Gironde estuary, even though highly dominated by refractory terrestrial material, shows an upstream-downstream gradient. The proportions of refractory terrestrial material show decrease from 92-84% upstream (pk30) to 79-66% in the lower estuary (pk86), whereas phytoplankton contribution increases inversely, from ca. 2% at pk30 to ca. 30% at pk86HT (Fig. 3 and 5). At pk86, the downstream station, POM shows higher PUFA proportions (i.e. primary producers, Fig. 2) and FA profiles are closer to the marine station one (Fig. 4). Another characteristic of this gradient is the higher bacterial contribution to the upstream POM as shown by decreasing BrFA proportions from ca. 10% at pk30LT to ca. 6% at the downstream station (Fig. 2 and 4). POM composition and FA profiles also differ between tides, especially at pk86, with more phytoplankton and less bacteria at high tide (Fig. 2 and 5). The observed patterns of POM composition in the Gironde estuary can be attributed to four different processes (Savoye et al., 2012 and references therein): 1) the overall mixing between fresh- and seawater, 2) the fresh water input upstream, 3) the formation and presence of an intense maximum turbidity zone due to the tide asymmetry and the macrotidal regime of the system, which extends from the upstream to the middle estuary, and 4) the phytoplankton production. The combination of these four processes explains the continent-ocean gradient within the Gironde estuary: riverine inputs bring riverine phytoplankton and litter (labile terrestrial material) in the upper estuary; the intense maximum turbidity zone is mainly located in the upper and middle estuary; it sequestrates the particles for one to two years, which allows the particles to highly degrade and thus leads to refractory terrestrial material; this material can be exported downstream; the large particle concentration and consequently the high turbidity of this zone is a great substrate for bacteria and prevent primary production, respectively; in the lower estuary, the decrease in turbidity allows local phytoplankton production; marine phytoplankton is also found there because of water mass mixing. The assumption of a strong bacterial activity in the Gironde estuary has been described by Savoye et al., (2012) as well as worldwide in other turbid estuaries (Bourgoin and Tremblay, 2010; Crump et al., 1998; Middelburg and Herman, 2007). Degraded material is often associated to more particles in the water column, providing more substrate for bacteria.

The continent-ocean gradient observed at multisystem scale in POM composition is illustrated by a phytoplankton-dominated POM *versus* a degraded POM characterized by strong bacterial contribution. Along this gradient, the specificities of each station influencing on POM composition (i.e. tidal influence) is also highlighted as pictured by station pk86. Indeed, POM composition at this station is an intermediate between typical estuarine and marine ones and bears either characteristics of marine influence at high tide with a larger contribution of phytoplankton (30%, Fig. 3) or a continental influence at low tide, with larger contribution of refractory terrestrial material (79%, Fig. 5) and bacteria (Fig. 2) from upstream. The association of higher bacterial contribution with refractory / degraded terrestrial material is typical of turbid estuaries, however, it is commonly admitted that bacteria are also largely represented in marine systems. This pattern can be obscured by temporal variability and a detailed analysis of POM composition over the annual cycle could reveal the dynamic of this source in association within the POM pool.

4.2. Seasonality

In order to identify a seasonality in POM composition and to which period higher bacterial contribution is associated, temporal variability of POM composition was investigated at a local scale, for each combination of station x tide independently. A constraints agglomerative hierarchical clustering analysis (CAHC) was performed on FA data (Fig. 6), with the average contribution of each source to the POM pool computed (mixing models) for each period (pie charts, Fig. 6). A PCA on FA profiles including the previously defined periods was also completed in order to identify specific FA patterns (Fig. S2). Over the annual cycle, a seasonal *versus* non-seasonal pattern of POM composition is observed along the previously identified spatial gradient. A typical 'summer period' *versus* 'winter period' seasonality is identified for the marine and downstream estuarine (pk86) stations. No seasonal pattern is observed for the upper and middle estuarine stations (pk30 and pk52).

The seasonal pattern of POM composition over the annual cycle identified for the stations of Arcachon lagoon, bay of Banyuls and pk86 opposes a 'summer period' to a 'winter period' which exact timing varies depending on the system (Fig. 6). The summer period is characterized by a strong contribution of MUFA and PUFA (especially C_{16} and C_{18}, Fig. S2) which are typical markers of pelagic and benthic primary producers as described in 4.1. (Dalsgaard et al., 2003; Kelly and Scheibling, 2012 and references therein), a pattern observed especially for the Arcachon lagoon. POM composition calculated by mixing models also reveals a large contribution of phytoplankton (87% in Arcachon lagoon, 62% in the bay of Banyuls), or higher contribution of this source compare to the rest of the year (pk86 from 39% at LT and 47% at HT) (Fig. 6). At pk86, the POM of the summer period also shows FA profiles similar as 'marine' profiles (Fig. 6, Fig S2). For the 3 stations, this period is clearly separated from the winter period, where contributions of SFA (mainly 13:0, 15:0, 17:0 but also 16:0 and 18:0) and BrFA (15:0iso, 15:0 anteiso, 17:0anteiso) as markers of detrital material and bacterial (e.g. Desvilettes et al., 1997; Mortillaro et al., 2012) are relatively higher (Fig. 6 and Fig. S2). During winter period, POM is mainly composed of refractory terrestrial material at pk86 (88% at LT, 71% at HT) or of river and benthic POM for the bay of Banuyls and Arcachon lagoon (respectively 17 and 21%, all benthic sources together, Fig. 6). The increase of bacterial, benthic and/or river sources to POM at wintertime has been widely described in the literature for diverse coastal systems (e.g. Gao et al., 2014, Yangtze River estuary; Malet et al., 2008, Marennes-Oléron; Lowe et al., 2014, San Juan Archipelago). This observed pattern is mainly related to seasonal variations in meteorological conditions such as 1) higher river flows responsible for more terrestrial inputs (e.g. Berto et al., 2013; Lebreton et al., 2016, Sanchez-Vidal et al., 2013; Xu and Jaffé, 2007) and 2) winter storms (i.e. stronger wind and currents) leading to higher resuspension of benthic material (e.g. Le Boyer et al., 2013; Lucas et al., 2000).

Within this seasonal pattern, a 'transition' period is also identified and corresponds to a spring period, before summer period. It is characterized by an increase of primary producer sources and a decrease in river and/or terrestrial sources contributions compare to winter period. In Arcachon lagoon, POM composition is mainly characterized by an increase of benthic primary producers (ca. 50%, both macrophytes and microphytobenthos, Fig. 6) whereas in the bay of Banyuls an increase of pelagic primary producers especially diazotrophs (from 13 to 26%) associated with a decrease of river POM contribution is observed (Fig. 6). At pk86, POM shows markers of bacteria and detrital material (e.g. 15:0iso, 15:0anteiso, 12:0, 20:0) and an increase of primary producers (22% at LT) (Fig. 6, Fig. S2). In general, for this period, FA profiles for all stations shows no specific pattern (Fig. S2) and a large variability in POM composition linked to system specificities. It likely reflects highly dynamic seasonal changes in structure of phytoplanktonic communities (i.e. taxonomic composition) (i.e. Lowe et al., 2014; Moynihan et al., 2016).

Finally, a less pronounced seasonality in POM composition is observed for station pk30 and no clear seasonal pattern for pk52. For both stations, POM is characterized by a highly homogeneous refractory-dominated POM (ca. 82 to 100 % for both stations), over the annual cycle, except for a short spring period (spring floods, around March) during which labile terrestrial POM (i.e. litter) and phytoplankton (i.e. freshwater) contribution increase (up to 27% and 7% respectively, Fig. 6, Fig. S2). The large variability in FA profiles at the two stations (Fig. S2) makes difficult to identify specific patterns using these proxies and differences does not allow clearly discriminating POM origin using FA profiles. The occasional nature of spring floods in this system and the relatively fresh characteristic of the OM brought during these events leads to its rapid degradation within the maximum turbidity zone of the estuary (Abril et al., 2002; Etcheber et al., 2007), which can explain the variability observed in FA profiles. Permanent mixing associated to strong OM degradation likely due to heterotrophic processing (Middelburg and Herman, 2007) occurring within the water column of the upstream and middle estuarine stations are likely driving the POM patterns observed over the annual cycle.

Both FA profiles and POM composition from mixing models calculations reveal a gradient of seasonality in POM composition along the previously identified continent-ocean spatial gradient. On one hand, marine systems show contrasted seasonality with a summer period characterized by a phytoplankton-dominated POM *versus* a winter period with increased river and/or benthic material and bacteria. On the other hand, the upstream and middle estuarine stations exhibit a less pronounced or absent seasonality and homogeneous refractory-dominated POM over the year with some occasional inputs of fresh material (i.e. labile terrestrial OM, freshwater phytoplankton).

POM composition of pk86 exhibits a seasonal pattern as for marine stations, being again an intermediate on the continent-ocean gradient. The observed patterns over the annual cycle for the studied systems are mainly driven by seasonal variation in hydrological (e.g. floods) and meteorological conditions (e.g. winter storms). In line with multisystem results, bacterial contribution is higher during winter period characterized by more degraded terrestrial material (i.e. river POM) and seems to be linked with degrading POM.

4.3. Bacterial contribution is linked to continental degraded POM

Bacterial compartment is often neglected in POM composition studies due to difficulties in both isolating bacterial cells from their substrate and identifying a specific signature. The present study reveal a continent-ocean gradient of bacterial contribution at multisystem scale (cf. 4.1.) and highlights the association of bacterial compartment with degraded POM (i.e. refractory terrestrial or river POM) (cf. 4.2.).

In order to confirm the hypothesis of a direct link between bacteria and degraded continental POM, the relationship between these two sources is tested in Figure 7. The relationship between each source and the different FA markers according to literature was verified (not shown). At multi-system scale, as described in 4.1., the contribution of bacteria to POM is higher for the estuarine stations, characterized by more continental degraded POM. Indeed, a positive relationship appears between the proportions of BrFA and the contribution of continental POM (i.e. refractory terrestrial or river POM, Fig. 7) both among all systems (R^2adj=0.66) and within marine ones (R^2adj=0.74; Arcachon lagoon, bay of Banyuls and pk86). Conversely, a negative relationship is observed between bacterial markers and pelagic primary producers (i.e. % contribution of primary producers; Fig. S3, R^2adj=0.69, all systems).

The relationship between bacteria and POM depends mainly on two considerations: Particle-attached bacteria are proportionally more abundant with the increase of substrate availability (i.e. quantity of suspended particles, Simon et al., 2002) but also with the quality of the available OM (i.e. POM lability, Crump et al., 2017). The spatial pattern observed of increasing bacterial contribution with continental POM is driven by the degree of turbidity of the systems (Crump et al., 1998): a larger amount of particles provides more substrate and food sources for microorganisms (Simon et al., 2002). Stronger hydrodynamic processes also lead to more resuspension of benthic bacteria. Despite of being a shallow tidal system, the Arcachon lagoon, has the lower bacterial contribution. It is a semi-enclosed lagoon protected from open-ocean currents and it receives low direct continental POM supply. In contrast, the bay of Banyuls is a non-tidal but open bay more influenced by continental POM inputs from the rivers of the Gulf of Lions (Tesi et al., 2007b; Higueras et al., 2014). Finally, the Gironde estuary, the largest Western-Europe estuary, is a tidal-dominated system is characterized by high and continuous mixing and sediment resuspension (Sottolichio and Castaing, 1999; Etcheber et al., 2007; Savoye et al., 2012). These characteristics account for the higher bacterial contribution in this system. Regarding OM quality, the higher occurrence of bacteria in relation with continental degraded POM has been reported in other studies using different biomarkers in both marine (Berto et al., 2013; Lowe et al., 2014) and estuarine (Bourgoin and Tremblay, 2010; Savoye et al., 2012) systems. Correlatives approaches have been tested to characterize this relationship and clearly demonstrate this link with degraded POM (Lowe et al., 2014) or to link bacterial production with material ongoing degradation processes (Crump et al., 2017), both studies taking into account for system peculiarities.

The inverse relationship observed between bacterial contribution and primary producers in systems impacted by seasonality (i.e. Arcachon lagoon, bay of Banyuls and pk86) reflects a switch in basal productivity: autotrophic spring and summer production provides most of the energy fuelling higher levels in the food webs, whereas winter period is likely associated the recycling of OM and high remineralisation due to heterotrophic activity (i.e. more bacteria). Conversely, in highly turbid systems dominated by refractory material such as the Gironde estuary, productivity is low and the balance of the ecosystem is in favour of heterotrophic processes (Abril et al., 2002). Terrestrial detritus has a low bioavailability for consumers, nevertheless, particle-attached bacteria acts as a central component for detrital food webs (Crump et al., 1998). Its high contribution to POM in the Gironde estuary makes the refractory material available as a possible food source for consumers at higher trophic levels (David et al., 2016). This has to be considered in carbon budgets.

The role of bacteria in degrading OM in oceanic and estuarine systems is well documented, however, a lack of knowledge remains regarding the actual contribution of this compartment to the POM pool and in carbon budgets. Indeed, none of the previously cited approaches allow for estimation in terms of carbon quantities. In the literature addressing this concern, the large variations in given estimated values for bacterial contribution to POM are likely due to the assumption used in quantitative approaches assuming the biomarker yield in samples follow bulk bacteria C and N contents. Also, establishing a link between bacterial specific FAs and bacterial biomass is complicated (Harvey and Macko, 1997) due to several contrary processes (production *vs* biomass turnover, biosynthesis *vs* degradation of specific compounds), therefore, this tool remains mainly qualitative when considered to estimate bacterial contribution in POM (e.g. Haack et al., 1994; Harvey and Macko, 1997). There is a need to better constraint the conversion factors between biomarkers and carbon quantities.

Difficulties mainly rise up from the fact that POM is already a mix of different sources (i.e. need to identify each source and its signature) where bacteria are attached to particles, leading to 1) difficulties in isolating bacterial cells from the POM matrix and to 2) identify its specific signature. In a study from Hansman and Sessions, (2015), $\delta^{13}C$ isotopic signature of different phytoplankton cells populations (e.g. Synechococcus, Diatoms) of *in situ* samples were determined by coupling fluorescence-activated cell sorting with a specialized micro-combustion interface and isotope-ratio mass spectrometry. This method could be applied to isolate bacterial cells and measure its isotopic signature. However, the authors raise few technical difficulties regarding the application of the method on the bacterial compartment. First, there is a necessity of adapting protocols (i.e. isolate bacteria from their substrate, pre-concentration) to get enough material of the targeted cell population for isotopic analyses. Second, as the cell sorting method is based on optical and florescence properties of the cells, labelling heterotrophic cells is required, being however aware of the possible impact of adding a carbon from a probe (i.e. LysoTracker Green or specific oligonucleotide FISH probes) on isotopic signature. Nevertheless, this approach remains very promising.

5. Conclusion

The present study establishes a clear positive relationship between bacterial biomass and degraded POM or POM undergoing degradation processes (i.e. refractory terrestrial and river POM) and an inverse relationship with primary producers. Bacterial contribution is higher in the turbid estuarine system (Gironde estuary) or during the winter period for systems characterized by a seasonal pattern (Arcachon lagoon, bay of Banyuls, pk86 the downstream station of the Gironde estuary). In addition to POM quality, turbidity (i.e. particles quantity) is a key process driving the observed spatial pattern in bacterial contribution to the pelagic POM.

Both fatty acid profiles and POM composition from mixing model calculations reveal the observed spatial and temporal patterns with different degrees of precision (i.e. seasonality better highlighted by stable isotopes), which confirms the relevance and the complementarity of using both methods to study POM origin and composition, including the bacterial compartment. With this multi-biomarkers approach, the present study clearly characterized POM composition and its relationship with bacterial compartment at large spatial scale and over the seasonal cycle.

The results of this study highlight the complexity behind POM origin and dynamic in the water column. Many biological and physiological processes are involved in POM composition, including remineralisation from bacteria, and are independently modulating the relationship between these two components. Depending on the POM sources and the bacterial contribution, the implications for the trophic pathways could be very different as suggested in the present study with the Gironde estuary. Similar studies in other estuarine and marine systems considering bacterial contribution to POM would help to better parametrize POM recycling in biogeochemical models and highlight the importance of this compartment in OM transfers within food webs.

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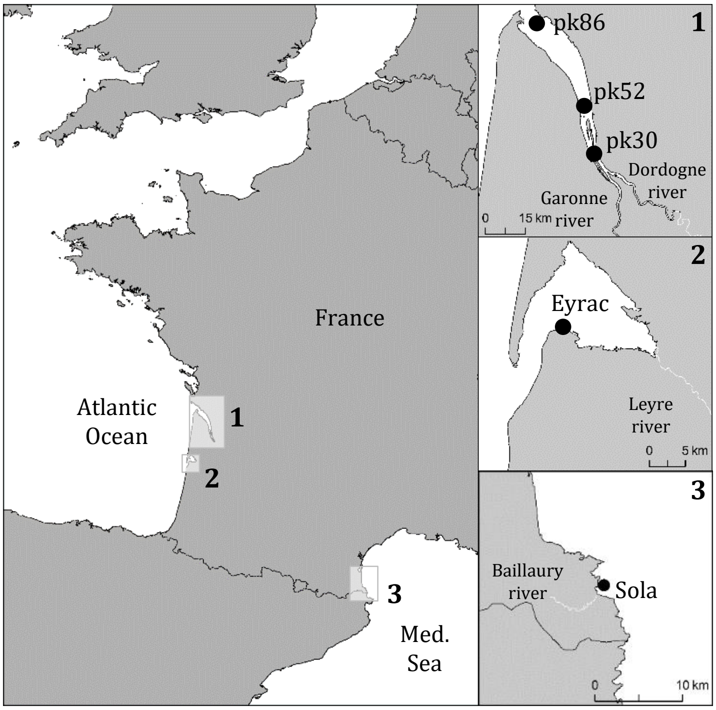

Figure 1: Studied systems and stations: 1. Gironde Estuary (3 stations: pk30, pk52 and pk86), 2. Arcachon Lagoon (Eyrac), 3. Bay of Banyuls (Sola) and their respective rivers. Med. Sea: Mediterranean Sea.

Source/station		Pelagic PP		Continental			Benthic PP		
		Phyto.	Diazo.	River.	Labile terr.	Refract. terr.	Macroalg.	Seagrasses	MPB
Arcachon lagoon	$\delta^{15}N$	5.2±1.2*	-	3.8±0.9*	-	-	9.8±1.6	6.6±1.2	4.0±0.6
	$\delta^{13}C$	-21.7±0.8*	-	-28.6±0.4*	-	-	-17.1±1.6	-12.3±1.7	-19.5±0.6
	C:N	7.1±0.8	-	15.0±1.7	-	-	11.6±4.1	22.0±3.7	9.8±0.7
Bay of Banyuls	$\delta^{15}N$	4.0±1.2	-1.2±0.9	5.2±1.0*	-	-	-	-	-
	$\delta^{13}C$	-22.7±1.0	-22.6±1.1	-27.4±0.6*	-	-	-	-	-
	C:N	6.9±1.6	6.9±1.5	8.5±1.6*	-	-	-	-	-
Gironde estuary	$\delta^{15}N$	-	-	-	-	-	-	-	-
	$\delta^{13}C$	-33.4 to -20.5*	-	-	-28.9±1.0*	-25.2±0.2	-	-	-
	C:N	7.5±1.6*	-	-	7.9±2.0*	8.7±0.7	-	-	-

Table 1: Elemental and isotopic signatures of carbon and nitrogen (mean±sd) of the considered organic matter sources used to run the mixing models for the three studied systems. Phyto.: phytoplankton, Diazo.: diazotrophes, River.: river POM, Labile terr: labile terrestrial POM, Refract. terr.: refractory terrestrial POM, Macroalg.: macroalgae, MPB: microphytobenthos, PP: primary producers.

*: values from modelled data (see Liénart et al., 2017). For the Gironde estuary, signatures were calculated following Savoye et al., (2012) and phytoplankton signature ranges from freshwater to marine phytoplankton.

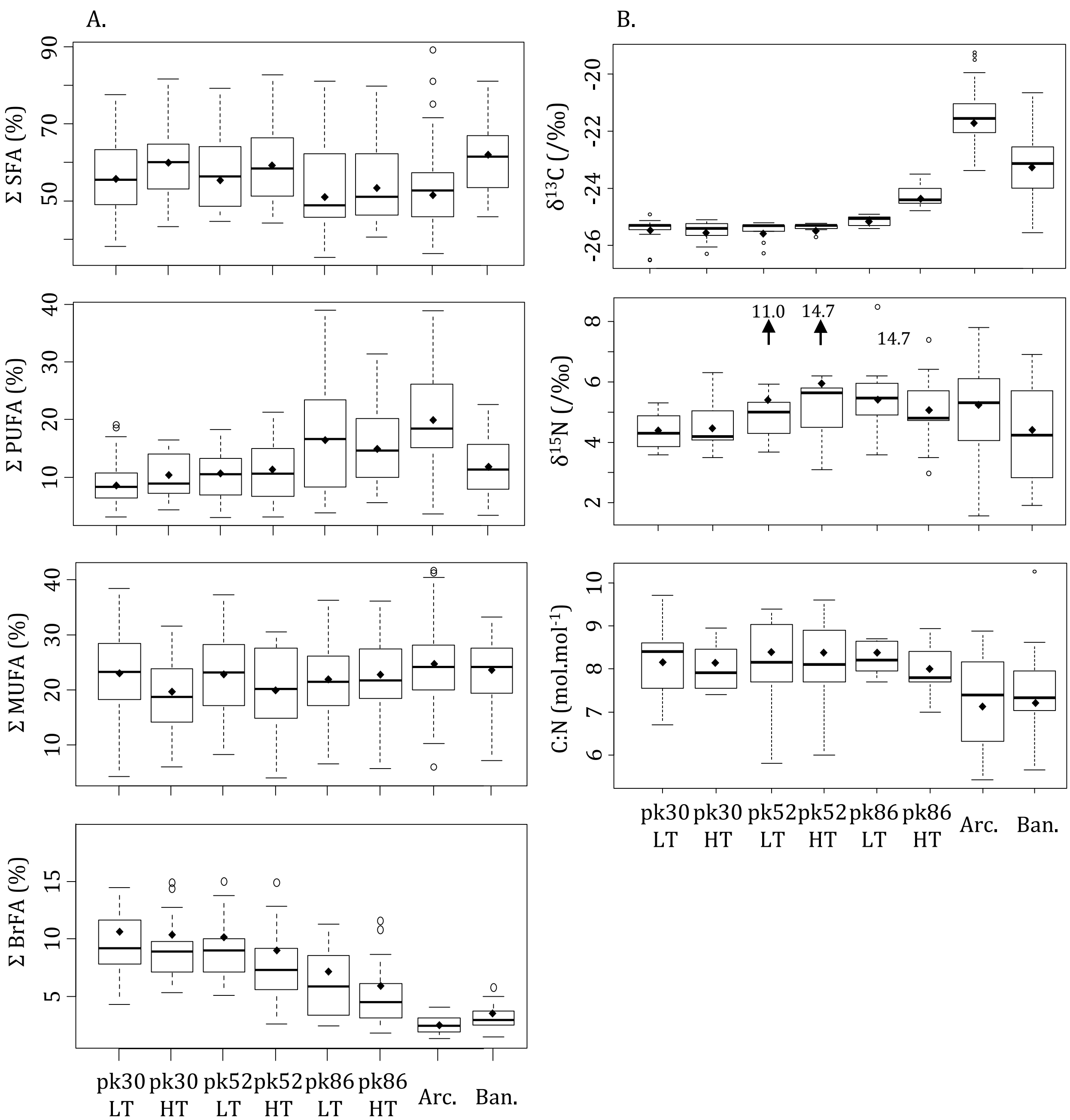

Figure 2: Boxplots for the 8 studied stations and tides over the entire annual cycle A. on FA classes in % of contribution to the total FA (left panel), B. on elemental and isotopic ratios of carbon and nitrogen ($\delta^{13}C$, $\delta^{15}N$, C:N) (right panel). SFA: saturated, MUFA: monounsaturated, PUFA: polyunsaturated, BrFA: branched. HT: high tide, LT: low tide for the Gironde estuary stations (pk30, n=11; pk52 and pk86 n=10), Ban.: bay of Banyuls (n=23 for SI, n=17 for FA), Arc.: Arcachon lagoon (n=22). See 2.1. for more information on sampling periods. Within the boxes medians are the black lines, means are black diamonds, first and third quartiles are hinges, outliers are black dots. Values over the vertical arrows indicate high values not shown at the boxplot scale.

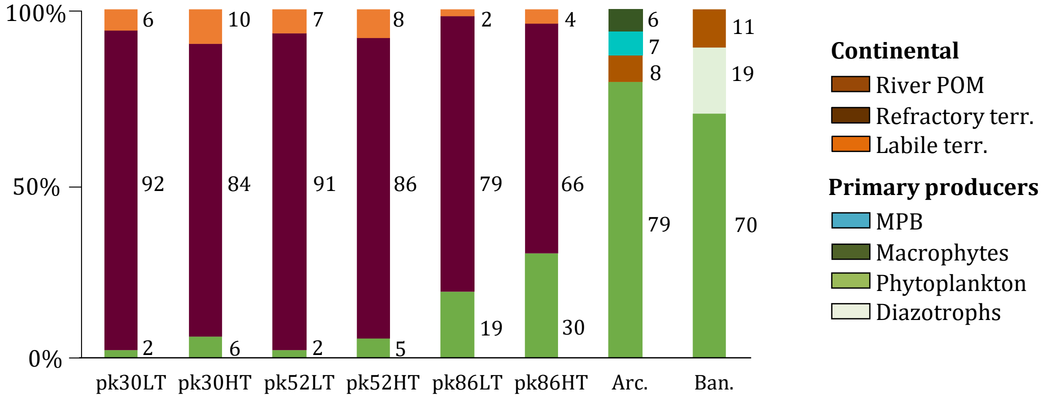

Figure 3: Mixing model outputs. Proportions of contribution of each source to the POM pool. Absolute uncertainty associated to the mixing-model outputs was usually close to 10%. Arc.: Arcachon lagoon. Ban.: bay of Banyuls. LT: low tide. HT: high tide. MPB: microphytobenthos

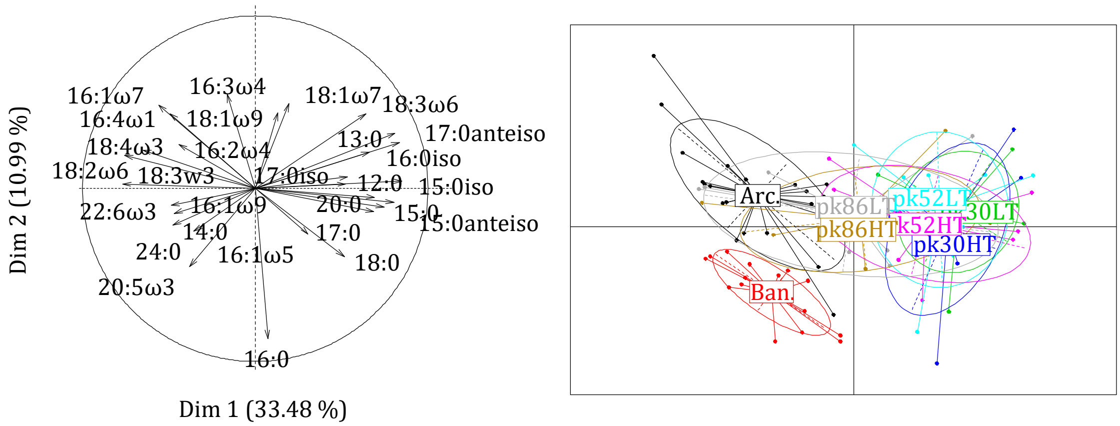

Figure 4: Principal component analysis (PCA) performed on FA data. Left panel: variables (individual FA), right panel: individual samples grouped by station. Arc.: Arcachon lagoon. Ban.: bay of Banyuls. HT: high tide. LT: low tide.

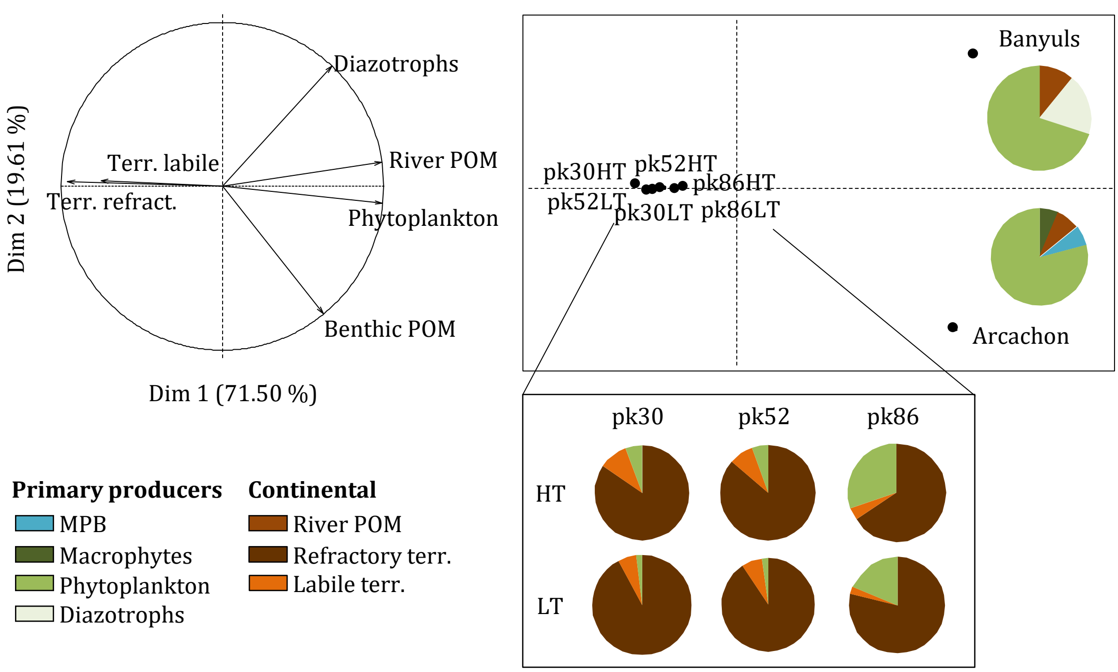

Figure 5: Principal component analysis (PCA) performed on POM composition proportions data computed by mixing models on isotopic data. Left panel: variables (sources of POM), right panel: the stations. Diagrames illustrates POM composition for each station showing mean annual percentage of each source over the studied period. MPB: microphytobenthos. LT: low tide, HT: high tide. Benthic POM: microphytobenthos (MPB) + macrophytes. Terr.: terrestrial.

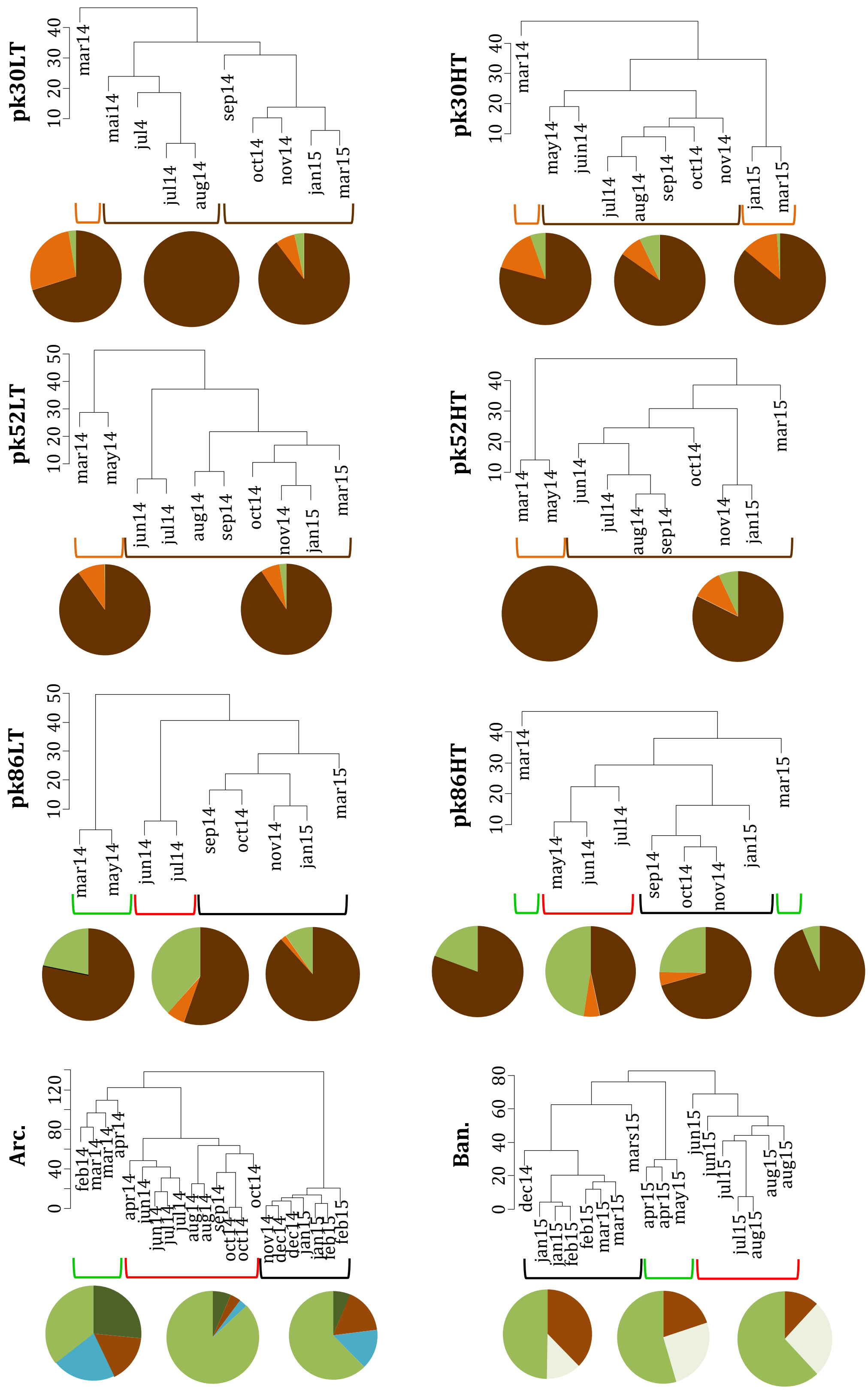

Figure 6: Constraint agglomerative hierarchical classification defining periods based on FA profiles. Pie charts illustrate POM composition (mixing models outputs) mean percentage of each source over each period. Arc.: Arcachon lagoon. Ban.: bay of Banyuls. HT: high tide: LT: low tide. For pie chart legend, see Fig 5. Red: productive period, black: low-productive period, green: transition period, orange: spring flood, brown: homogeneous POM composition on a unique period.

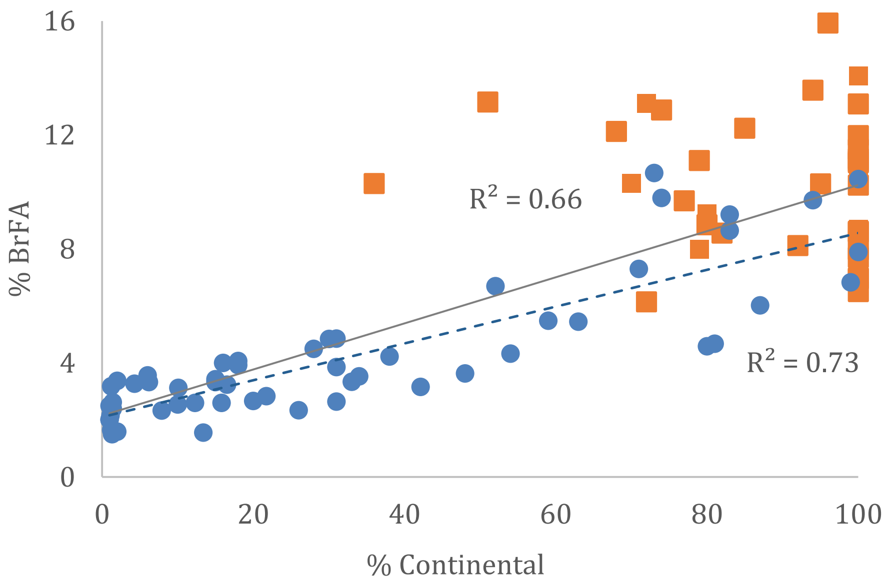

Figure 7: relationship between the % of bacterial FA markers (BrFA) of TFA and the % of Continental POM (i.e. refractory terrestrial or river POM) for all sampling dates of all stations (R^2adj.=0.66, grey full line), all marine stations (blue circles, Arcachon lagoon, bay of Banyuls and pk86 HT and LT, R^2adj.=0.74, blue dashed line) and the upper estuarine stations (orange squares, pk30 and pk52 HT and LT).