
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 C-13, delta N-15) 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.

Highlights

► Fatty acids, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are used to link bacterial-derived OM and POM. ► Bacterial OM is higher in turbid systems characterized by refractory terrestrial POM. ► Bacterial OM is higher in winter for seasonal systems and linked to river/benthic POM. ► Bacterial and degraded/in degradation OM show positive relationship for all systems.

Keywords : POM dynamic, Bacteria, delta C-13, delta N-15, Fatty acids, Mixing models, French littoral

41 1. Introduction

42 Coastal systems are amongst earth's most productive systems (Duarte & Cebrián, 1996;
43 Gattuso et al., 1998) promoting an intense biological and biogeochemical activity (Smith
44 and Hollibaugh, 1993) responsible for production and exchange of matter between land
45 and sea. Coastal systems generate 12% of oceanic primary production (Dunne et al.,
46 2007) and a non-negligible part of matter inputs originate from rivers as dissolved or
47 particulate material (Ludwig et al., 1996). In addition, organic matter (OM) fluxes are
48 largely induced or regulated by living organisms (i.e. primary and secondary production,
49 remineralization, etc.). Within these systems, suspended particulate organic matter
50 (POM) is a result of multiple inputs from adjacent compartments. POM is composed of
51 numerous sources of organic carbon including phytoplankton, bacteria, benthic macro-
52 and micro- primary producers, terrestrial OM from river inputs (Liénart et al., 2017;
53 Tesi et al., 2007a; Volkman and Tanoue, 2002). However, the diversity of sources and
54 the numerous process acting on POM composition and dynamics make difficult to
55 characterize and quantify the contribution of each source to the POM pool. In addition,
56 within these sources, bacterial compartment is often neglected.

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

79 Investigating bacteria in the ocean has always been methodologically challenging. Single
80 cells are difficult to isolate due to their small size but also due to the complex mixture of
81 particles in seawater (e.g. phytoplanktonic cells, detritus; Kemp et al., 1993). The most
82 common approach to estimate the contribution of a given organic matter source in
83 carbon budgets or in a POM pool is to use stable isotopes (SI) ratio of carbon and
84 nitrogen ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), C:N elemental ratio or other biomarkers such as fatty acids (FA) as
85 OM tracers (e.g. Connelly et al., 2016; Dubois et al., 2014; He et al., 2014; Lowe et al.,
86 2014). Thanks to the distinct signatures of the sources (e.g. marine *versus* continental,
87 different primary producers), elemental and isotopic ratios have been used in
88 numerous studies characterizing the origin and composition of POM in coastal systems
89 and even to quantify the contribution of each source to the POM pool by using mixing
90 models (e.g. Berto et al., 2013; Cresson et al., 2012; Liénart et al., 2017). However,
91 classical isotopes studies (i.e. on 'bulk' POM from field samples) cannot attempt
92 estimating the contribution of bacterial biomass to the POM pool: isotopic signature of
93 both bacteria and its substrate is supposed to be identical.

94 Among other, FAs appear to be a relevant proxy to reveal the bacterial biomass. These
95 compounds are the main structural components of cell membranes, a high source of
96 metabolic energy and are, in many circumstances, conservatively preserved in cells
97 contrarily to other molecules (e.g. proteins) (Dalsgaard et al., 2003). Moreover, FAs
98 biosynthesis varies depending on the targeted organisms (e.g. primary producers,
99 consumers, bacteria) making single FA a suitable tool (trophic marker, concept of
100 FATM) for the identification of taxonomic groups (Dalsgaard et al., 2003) and to trace
101 its transfer along food webs (e.g. Hall et al., 2006; Kelly and Scheibling, 2012). Branched
102 FA (BrFA) are typically synthesized by bacteria (Dalsgaard et al., 2003; Rajendran et al.,
103 1993; Volkman et al., 1980) and more specifically, C₁₅ and C₁₇ iso- and anteiso- (15:0iso,
104 15:0anteiso, 17:0iso, 17:0anteiso) are described as markers of bacterioplankton (Budge
105 and Parrish, 1998; Desvillettes et al., 1997; Hall et al., 2010). Among others, FAs
106 biomarkers have been used to discriminate phytoplankton from macroalgae in marine
107 sediments (Hu et al., 2006; Meziane et al., 2006, 1997), to distinguish autochthonous (i.e.
108 primary production) from allochthonous (i.e. terrestrial OM) sources of POM in coastal
109 waters (Lowe et al., 2014; Xu and Jaffé, 2007) and to investigate bacterial contribution
110 as food source (Meziane et al., 2002).

111 There is an increasing interest in characterizing POM pool composition but only few
112 studies discussed and tried to estimate bacterial biomass contribution to pelagic POM
113 (e.g. Berto et al., 2013; Bourgoïn and Tremblay, 2010; Savoye et al., 2012). The present
114 study proposes to estimate the relationship between bacterial compartment and POM in
115 surface water of five stations belonging to three coastal systems with different
116 biological, biogeochemical and geomorphological characteristics. It aims evaluating the
117 link between bacteria and the different POM sources 1) at multisystem scale,
118 considering system types and 2) over the seasonal cycle, at local scale, by using two
119 complementary approaches: fatty acids biomarkers, which is the core of this study, and
120 elemental and isotopic ratios of carbon and nitrogen (as in Liénart et al., 2017). Spatial

121 and temporal variability of bacterial contribution are expected to be linked with those
122 of OM sources and more particularly, bacterial biomass is expected to be high in
123 systems characterized by an intense biogeochemical activity (homogeneous POM
124 composition due to heterotrophic processing, i.e. Middelburg and Herman, 2007) or
125 with higher turbidity (more particles as substrate, i.e. Simon et al., 2002). Bacterial
126 contribution is also expected to increase with more degraded material or OM
127 undergoing degradation processes (Abril et al., 2002), during winter or just after inputs
128 of fresh organic material.

129 **2. Materials and methods**

130

131 **2.1. Study systems and sampling**

132 Five stations belonging to three systems (**Fig. 1**) characterized by different
133 geomorphological features and biogeochemical properties (salinity ranges, turbidity,
134 trophic status, etc.) were sampled for surface water (c.a. 1m depth water) for the years
135 2014-2015. Two systems are located on the Atlantic coast: the Gironde estuary, a
136 macrotidal, turbid and eutrophic estuary, and Arcachon lagoon, a mesotidal,
137 mesotrophic semi-enclosed lagoon. The third system is located on the Mediterranean
138 coast: the oligotrophic open bay of Banyuls-sur-mer. The Gironde estuary was monthly
139 sampled at high (HT) and low (LT) tides at three stations (from upstream to
140 downstream: pk30, pk52, pk86) along the salinity gradient (c.a. 0-30) from March 2014
141 to March 2015. As high and low tide sampling of a single station correspond to the
142 sampling of different water masses, each combination tide x station was considered as
143 independent to each other, just like if six different stations were sampled. Arcachon
144 lagoon (station Eyrac) was bi-monthly sampled at high tide from February 2014 to
145 February 2015. The bay of Banyuls (station Sola) was bi-monthly sampled from
146 December 2014 to August 2015. For a better understanding, system's name are used to
147 describe our study sites.

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

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

160 2.2. Fatty acid extraction and analysis

161 The method used for the Fatty Acids (FA) extraction follows largely the Bligh and Dyer
162 method (1959) as adjusted in Meziane et al., (2006). To quantify FA concentrations, a
163 known volume of a commercial internal standard (C23:0, concentration of 5 mg/mL)
164 was introduced in each sample. For POM and SOM analyses, half-filters were soaked in a
165 distilled water-chloroform-methanol solution (1:1:2, v:v:v) and sonicated during 20
166 minutes for the FAs extraction. Samples were thereafter completed by a distilled water-
167 chloroform solution (1:1, v:v) and centrifuged (3 000 rpm, 5 minutes). Lipid phases
168 were transferred in others tubes, completed by a distilled water-chloroform solution
169 (1:1, v:v) and sonicated again during 20 minutes in order to maximize the extraction.
170 Then, samples were evaporated under a dinitrogen (N₂) flux, diluted a second time in a
171 mixture of methanol and sodium hydroxide (2:1, v:v; [NaOH] = 2 mol.L⁻¹) and heated at
172 90°C during 90 minutes for FAs saponification. Finally, FAs were converted into FA
173 methyl esters after (FAME) for ten minutes at 90°C using a methanolic boron trifluoride
174 solution (BF₃-CH₃OH 14%, 1 mL). At the end of the reaction, the chloroform phase
175 containing FAMES was retrieved and stored at - 20°C.

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

$$183 \quad C_{FAME} = \left(\frac{A_{FAME}}{A_{C23}} \times \frac{C_{23}}{M_f} \right)$$

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

187 2.3. Stable isotopes analysis

188 Within the scope of the SOMLIT coastal monitoring program, surface water was
189 sampled, processed and analysed for elemental and isotopic ratios of C and N (δ¹³C,
190 δ¹⁵N, C:N) following standardized protocols available on the SOMLIT website
191 (<http://somlit.epoc.u-bordeaux1.fr/fr/spip.php?rubrique13>). Existing datasets of the
192 targeted parameters used in this study were retrieved from the SOMLIT database
193 (<http://somlit.epoc.u-bordeaux1.fr>). More information concerning stable isotope
194 analysis are also available in Liénart et al., (2017).

195 2.4. Numerical analysis

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

198 **2.4.1. Biomarker data pre-treatment**

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

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

208 **2.4.2. Organic matter sources and mixing models**

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

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

232 To avoid bias and to minimize the uncertainty associated to the mixing-model outputs,
233 only relevant sources were used as end-members in each studied system, based on

234 previous studies and mathematical considerations (e.g. Fry 2013, Phillips and Gregg
235 2003). Mixing models based on a Bayesian approach (SIAR package; trophic enrichment
236 factor = 0, siarsolomcmcv4; Parnell et al., 2010) were run for each sampling date and
237 each station by using isotopic ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and elemental (N:C ratio) values of sources
238 and bulk POM for the Arcachon lagoon and the bay of Banyuls. The absolute uncertainty
239 associated to the mixing-model outputs was usually close to 10%. For the Gironde
240 estuary, the $\delta^{15}\text{N}$ and C:N ratio does not allow the discrimination of the sources in this
241 specific system. Thus, $\delta^{13}\text{C}$ and the ratio of POC to suspended particulate matter were
242 used to calculate the relative proportion of each sources at each sampling date for each
243 station following the approach developed by Savoye et al., (2012) for this specific
244 system.

245 **2.4.3. Multivariate analysis**

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

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

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

263 **3. Results**

264 **3.1. Fatty acids**

265 Fifty-eight individual fatty acids were identified over all POM samples: 38 for the
266 estuarine POM, 41 for Arcachon lagoon POM and 48 for the bay of Banyuls POM
267 (**Supplementary Table 1**). Most of the identified FAs were $\leq \text{C}_{20}$ chains, representing ca.
268 95% of the total fatty acids (TFA). For all the stations, each individual contribution of 5
269 FAs exceeded 10% of TFA: 14:0, 16:0, 16:1 ω 7, 18:0 and 19:1 ω 9. The combination of
270 these 5 FAs represented in average 61 to 67% of the TFA depending on the station.
271 Secondary FAs identified (i.e. FAs with individual contribution ranging from 1 to 10% of
272 TFA) differ in terms of presence and contribution between stations. Nevertheless, the

273 essential fatty acids (EFA) 20:5 ω 3 and 22:6 ω 3 as well as 15:0, 15:0anteiso, 17:0anteiso,
274 16:1 ω 5, 16:1 ω 9, 18:1 ω 7, 18:2 ω 6, 18:3 ω 3, 18:4 ω 3 were generally identified at each
275 station.

276 Over the studied stations and tides, total saturated FA (SFA) contributed in average to
277 53 to 61% of the TFA. Total monounsaturated FA (MUFA) showed relatively constant
278 proportion (19 to 24%) whereas total polyunsaturated FA (PUFA) and branched FA
279 (BrFA) exhibited variable contributions (respectively ca. 9 to 20% and 2.5 to 10%) of
280 the TFA. No significant differences in SFA contribution were found between stations
281 except between the bay of Banyuls and Arcachon lagoon (KW, posthoc Nemenyi test,
282 $p < 0.05$; Fig. 2, A). MUFA contribution was not significantly different between the
283 studied stations (Fig. 2, A). PUFA contribution was significantly higher (KW, posthoc
284 Nemenyi test, $p < 0.05$) for Arcachon lagoon than for the upstream and middle estuarine
285 stations at high and low tides (pk30HT, pk30LT, pk52HT, pk52LT) as well as with the
286 bay of Banyuls (Fig. 2, A). BrFA contribution was significantly lower (KW, posthoc
287 Nemenyi test, $p < 0.01$) for Arcachon lagoon and the estuarine stations at high and low
288 tides and for the bay of Banyuls and the upper and middle estuarine stations at high and
289 low tides (Fig. 2, A). It clearly appeared that 1) there was a gradient of PUFA and BrFA
290 along the Gironde estuary and 2) the bay of Banyuls exhibited intermediate values
291 compared to the estuarine stations on the one hand and Arcachon lagoon on the other
292 hand.

293 3.2. Elemental and isotopic ratios of POM and organic matter sources

294 C:N ratio of POM was in average 7.8 mol.mol⁻¹ with values ranging from ca. 5 to 10
295 mol.mol⁻¹ (Fig. 2, B), with higher average values for the estuarine stations (ca. 8
296 mol.mol⁻¹) than for the marine stations (ca. 7.3 mol.mol⁻¹). POM $\delta^{15}\text{N}$ was in average ca.
297 5‰ with values ranging from ca. 1.5 (bay of Banyuls) to more than 8 in the Gironde
298 estuary (Fig. 2, B); the Mediterranean station of the bay of Banyuls exhibited the lowest
299 average value (ca. 4.2‰). No significant differences were found between the stations
300 for these two parameters. POM $\delta^{13}\text{C}$ values ranged between -26‰ and -19‰.
301 Significant differences (KW, posthoc Nemenyi test, $p < 0.05$) were found between
302 Arcachon lagoon and the estuarine stations except pk86HT, and between the bay of
303 Banyuls and pk30 and pk52 at both tides (Fig. 2, B). It clearly appeared that 1) there
304 was an overall gradient of isotopic ratios along the Gironde estuary and 2) the bay of
305 Banyuls exhibited intermediate values compared to the estuarine stations on the one
306 hand and Arcachon lagoon on the other hand.

307 In each studied system, elemental and/or isotopic ratios enable discriminating each
308 organic matter source and allow the use of mixing models in order to quantify the
309 proportion of each source within the POM (Table 1; Savoye et al., 2012; Liénart et al.,
310 2017; see 2.4.2).

311 3.3. POM composition

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

322 4. Discussion

323 4.1. A continent-ocean gradient

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

329 At a multisystem scale, the estuarine stations of the Gironde (pk86, pk52 and pk30) are
330 opposed to the marine stations of the bay of Banyuls and Arcachon lagoon. This
331 gradient is observed with both fatty acids (PCA Fig. 4, axis 1) and POM composition data
332 (PCA Fig. 5, axis 1). In the estuarine stations, POM is characterized by a dominance of
333 refractory terrestrial material (i.e. 83% average for all stations and tides, Fig. 5), which
334 is a typical feature of the Gironde estuary (Etcheber et al., 2007; Savoye et al., 2012). FA
335 profiles show larger contribution of SFA (12:0, 13:0, 15:0, 18:0, Fig. 4) and lower of
336 PUFA, which is typical of degraded POM as PUFA and MUFA are rapidly degraded in
337 aquatic systems (Meyers, 2003; Saliot et al., 2001) compare to SFA (Meyers and Eadie,
338 1993). The relative proportions of these groups of FA in a POM pool is thus used as
339 indicator of its freshness or degradation level (Canuel, 2001; Mortillaro et al., 2011).
340 Compared to marine systems, POM in the estuary is also associated to a higher bacterial
341 biomass reflected by a larger contribution of BrFA (Fig. 4; Fig. 2; typical markers:
342 15:0iso, 15:0anteiso, 16:0iso, 17:0anteiso, Rajendran et al., 1993; Volkman et al., 1980).
343 The Gironde estuary is a 'tidal-dominated' estuary (Middelburg and Herman, 2007)
344 characterized by high turbidity and long residence time of particles which induce low
345 primary production and intense remineralisation (Abril et al., 2002, 1999; Etcheber et
346 al., 2007) and leads to the typical observed POM profiles. Increasing contribution of
347 bacteria and related FA markers with larger amounts of detrital / refractory material
348 have been illustrated by other authors (i.e. Lowe et al., 2014; Mortillaro et al., 2012). By
349 opposition, phytoplankton dominates POM composition in marine systems from 70% at
350 the bay of Banyuls to 79% in Arcachon lagoon (Fig. 5). In open ocean but also in coastal
351 marine systems, phytoplankton is the major source of POM (Bode et al., 2006; Cresson
352 et al., 2012; Lebreton et al., 2016; Liénart et al., 2017, 2016; Lowe et al., 2014) which

353 relative contribution varies over space and time (Liénart et al., 2017). In the bay of
354 Banyuls and Arcachon lagoon, POM is likely 'fresh' (i.e. alive phytoplanktonic cells),
355 characterized by a higher contribution of 16:1 ω 7 and the PUFAs 16:4 ω 1, 18:2 ω 6,
356 18:3 ω 3, 18:4 ω 3, 20:5 ω 3 and 22:6 ω 3 (Fig. 4). Primary producers are organisms capable
357 to *de novo* produce PUFAs, ω 3 and ω 6 with long carbon chain such as the EFA 20:5 ω 3
358 and 22:6 ω 3 (e.g. Cook 1996; Sargent and Henderson, 1995), or to add double bonds and
359 extend carbon chains from SFA or MUFA (Dalsgaard et al., 2003). The association of
360 these FAs in the POM pool emphasize the dominance of primary producers in the two
361 marine systems as similarly found by Lowe et al., (2014) and Mortillaro et al., (2012).

362 Within marine stations, the contrast between Arcachon lagoon and the bay of Banyuls is
363 observed with both FA (PCA Fig. 4, axis 2) and POM composition (PCA Fig. 5, axis 2)
364 even though more precisely described by FA profiles. At Arcachon lagoon, higher
365 contributions of 16:1 ω 7, 16:4 ω 1 and 18:4 ω 3 (Fig. 4) show the presence of some
366 macroalgae and diatoms (Dalsgaard et al., 2003; Kelly and Scheibling, 2012 and
367 references therein) and 18:2 ω 6, 18:3 ω 3, 18:4 ω 3 and 22:6 ω 3 (Fig. 4) of macrophytes
368 and associated epiphytes at different degradation stages. These FA reflects benthic OM
369 influence, a similar pattern also identified by Dubois et al., (2014) in this system.
370 Typically, in shallow systems, benthic contribution to the surface water POM can be
371 high due to strong benthic-pelagic coupling processes (Malet et al., 2008; Modéran et al.,
372 2012). In Arcachon lagoon, a shallow (ca. 8m at Eyrac) semi-enclosed lagoon under tidal
373 influence, macrophytes and benthic microalgae that are widely developed and
374 significantly fuel the POM pool (e.g. Dubois et al., 2012; Schaal et al., 2008, Fig. 5) due to
375 resuspension processes (e.g. Dubois et al., 2012; Liénart et al., 2018). By contrast, the
376 bay of Banyuls shows a POM composition dominated by pelagic primary producers (i.e.
377 phytoplankton and diazotrophs: 89% total, Fig. 5) even though FA markers of
378 phytoplankton are less represented than in Arcachon lagoon (Fig. 4). The oligotrophic
379 Mediterranean Sea is characterized by the presence of atmospheric N₂-fixing organisms
380 in phytoplankton communities (i.e. diazotrophs, Kerhervé et al., 2001; Zeev et al., 2008)
381 that are able to cope with N limitation and have a non-negligible contribution to the
382 POM pool (19%, Fig. 5). However, as primary producers, N₂-fixing organisms have FA
383 profiles identical to the 'classical' phytoplankton ones (i.e. C14, C16, 18:1 ω 9) (Carpenter
384 et al., 1997; Vargas et al., 1998) leading to difficulties in identifying separate FA markers
385 for this source. In comparison to Arcachon lagoon, the POM of the bay of Banyuls has
386 lower proportions of PUFA (ca. 12 vs 21%, Fig. 2) and higher contributions of SFA (ca.
387 61 vs 53%, Fig. 2) and BrFA (3.6 vs 2.5%, Fig. 2). SFA indicate degraded material and, in
388 marine environments, of POM from terrestrial origin (e.g. Budge et al., 2001). The bay of
389 Banyuls is an open bay with water masses coming from the open ocean influencing on
390 its POM composition. In the Gulf of Lion, marine currents are mainly coming from the
391 east and carry particles from the surrounding rivers (Higuera et al., 2014) and more
392 particularly material from the Rhône River that can be detected far from the river
393 mouth (Tesi et al., 2007b). It explains the rather large inputs of continental (likely
394 degraded) material at this station (11%, Fig. 5) also reflected by the presence of some

395 specific FAs (e.g. 24:0, Fig. 4), and is consistent with the larger bacterial contribution
396 compare to Arcachon lagoon.

397 At local scale, POM composition of the Gironde estuary, even though highly dominated
398 by refractory terrestrial material, shows an upstream-downstream gradient. The
399 proportions of refractory terrestrial material show decrease from 92-84% upstream
400 (pk30) to 79-66% in the lower estuary (pk86), whereas phytoplankton contribution
401 increases inversely, from ca. 2% at pk30 to ca. 30% at pk86HT (Fig. 3 and 5). At pk86,
402 the downstream station, POM shows higher PUFA proportions (i.e. primary producers,
403 Fig. 2) and FA profiles are closer to the marine station one (Fig. 4). Another
404 characteristic of this gradient is the higher bacterial contribution to the upstream POM
405 as shown by decreasing BrFA proportions from ca. 10% at pk30LT to ca. 6% at the
406 downstream station (Fig. 2 and 4). POM composition and FA profiles also differ between
407 tides, especially at pk86, with more phytoplankton and less bacteria at high tide (Fig. 2
408 and 5). The observed patterns of POM composition in the Gironde estuary can be
409 attributed to four different processes (Savoye et al., 2012 and references therein): 1)
410 the overall mixing between fresh- and seawater, 2) the fresh water input upstream, 3)
411 the formation and presence of an intense maximum turbidity zone due to the tide
412 asymmetry and the macrotidal regime of the system, which extends from the upstream
413 to the middle estuary, and 4) the phytoplankton production. The combination of these
414 four processes explains the continent-ocean gradient within the Gironde estuary:
415 riverine inputs bring riverine phytoplankton and litter (labile terrestrial material) in the
416 upper estuary; the intense maximum turbidity zone is mainly located in the upper and
417 middle estuary; it sequesters the particles for one to two years, which allows the
418 particles to highly degrade and thus leads to refractory terrestrial material; this
419 material can be exported downstream; the large particle concentration and
420 consequently the high turbidity of this zone is a great substrate for bacteria and prevent
421 primary production, respectively; in the lower estuary, the decrease in turbidity allows
422 local phytoplankton production; marine phytoplankton is also found there because of
423 water mass mixing. The assumption of a strong bacterial activity in the Gironde estuary
424 has been described by Savoye et al., (2012) as well as worldwide in other turbid
425 estuaries (Bourgoin and Tremblay, 2010; Crump et al., 1998; Middelburg and Herman,
426 2007). Degraded material is often associated to more particles in the water column,
427 providing more substrate for bacteria.

428 The continent-ocean gradient observed at multisystem scale in POM composition is
429 illustrated by a phytoplankton-dominated POM *versus* a degraded POM characterized by
430 strong bacterial contribution. Along this gradient, the specificities of each station
431 influencing on POM composition (i.e. tidal influence) is also highlighted as pictured by
432 station pk86. Indeed, POM composition at this station is an intermediate between
433 typical estuarine and marine ones and bears either characteristics of marine influence
434 at high tide with a larger contribution of phytoplankton (30%, Fig. 3) or a continental
435 influence at low tide, with larger contribution of refractory terrestrial material (79%,
436 Fig. 5) and bacteria (Fig. 2) from upstream. The association of higher bacterial

437 contribution with refractory / degraded terrestrial material is typical of turbid estuaries,
438 however, it is commonly admitted that bacteria are also largely represented in marine
439 systems. This pattern can be obscured by temporal variability and a detailed analysis of
440 POM composition over the annual cycle could reveal the dynamic of this source in
441 association within the POM pool.

442 **4.2. Seasonality**

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

455 The seasonal pattern of POM composition over the annual cycle identified for the
456 stations of Arcachon lagoon, bay of Banyuls and pk86 opposes a 'summer period' to a
457 'winter period' which exact timing varies depending on the system (Fig. 6). The summer
458 period is characterized by a strong contribution of MUFA and PUFA (especially C₁₆ and
459 C₁₈, Fig. S2) which are typical markers of pelagic and benthic primary producers as
460 described in 4.1. (Dalsgaard et al., 2003; Kelly and Scheibling, 2012 and references
461 therein), a pattern observed especially for the Arcachon lagoon. POM composition
462 calculated by mixing models also reveals a large contribution of phytoplankton (87% in
463 Arcachon lagoon, 62% in the bay of Banyuls), or higher contribution of this source
464 compare to the rest of the year (pk86 from 39% at LT and 47% at HT) (Fig. 6). At pk86,
465 the POM of the summer period also shows FA profiles similar as 'marine' profiles (Fig. 6,
466 Fig S2). For the 3 stations, this period is clearly separated from the winter period, where
467 contributions of SFA (mainly 13:0, 15:0, 17:0 but also 16:0 and 18:0) and BrFA (15:0iso,
468 15:0 anteiso, 17:0 anteiso) as markers of detrital material and bacterial (e.g. Desvillettes
469 et al., 1997; Mortillaro et al., 2012) are relatively higher (Fig. 6 and Fig. S2). During
470 winter period, POM is mainly composed of refractory terrestrial material at pk86 (88%
471 at LT, 71% at HT) or of river and benthic POM for the bay of Banyuls and Arcachon
472 lagoon (respectively 17 and 21%, all benthic sources together, Fig. 6). The increase of
473 bacterial, benthic and/or river sources to POM at wintertime has been widely described
474 in the literature for diverse coastal systems (e.g. Gao et al., 2014, Yangtze River estuary;
475 Malet et al., 2008, Marennes-Oléron; Lowe et al., 2014, San Juan Archipelago). This
476 observed pattern is mainly related to seasonal variations in meteorological conditions
477 such as 1) higher river flows responsible for more terrestrial inputs (e.g. Berto et al.,

478 2013; Lebreton et al., 2016, Sanchez-Vidal et al., 2013; Xu and Jaffé, 2007) and 2) winter
479 storms (i.e. stronger wind and currents) leading to higher resuspension of benthic
480 material (e.g. Le Boyer et al., 2013; Lucas et al., 2000).

481 Within this seasonal pattern, a 'transition' period is also identified and corresponds to a
482 spring period, before summer period. It is characterized by an increase of primary
483 producer sources and a decrease in river and/or terrestrial sources contributions
484 compare to winter period. In Arcachon lagoon, POM composition is mainly
485 characterized by an increase of benthic primary producers (ca. 50%, both macrophytes
486 and microphytobenthos, Fig. 6) whereas in the bay of Banyuls an increase of pelagic
487 primary producers especially diazotrophs (from 13 to 26%) associated with a decrease
488 of river POM contribution is observed (Fig. 6). At pk86, POM shows markers of bacteria
489 and detrital material (e.g. 15:0iso, 15:0anteiso, 12:0, 20:0) and an increase of primary
490 producers (22% at LT) (Fig. 6, Fig. S2). In general, for this period, FA profiles for all
491 stations shows no specific pattern (Fig. S2) and a large variability in POM composition
492 linked to system specificities. It likely reflects highly dynamic seasonal changes in
493 structure of phytoplanktonic communities (i.e. taxonomic composition) (i.e. Lowe et al.,
494 2014; Moynihan et al., 2016).

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

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

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

526 **4.3. Bacterial contribution is linked to continental degraded POM**

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

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

543 The relationship between bacteria and POM depends mainly on two considerations:
544 Particle-attached bacteria are proportionally more abundant with the increase of
545 substrate availability (i.e. quantity of suspended particles, Simon et al., 2002) but also
546 with the quality of the available OM (i.e. POM lability, Crump et al., 2017). The spatial
547 pattern observed of increasing bacterial contribution with continental POM is driven by
548 the degree of turbidity of the systems (Crump et al., 1998): a larger amount of particles
549 provides more substrate and food sources for microorganisms (Simon et al., 2002).
550 Stronger hydrodynamic processes also lead to more resuspension of benthic bacteria.
551 Despite of being a shallow tidal system, the Arcachon lagoon, has the lower bacterial
552 contribution. It is a semi-enclosed lagoon protected from open-ocean currents and it
553 receives low direct continental POM supply. In contrast, the bay of Banyuls is a non-tidal
554 but open bay more influenced by continental POM inputs from the rivers of the Gulf of
555 Lions (Tesi et al., 2007b; Higuera et al., 2014). Finally, the Gironde estuary, the largest
556 Western-Europe estuary, is a tidal-dominated system is characterized by high and
557 continuous mixing and sediment resuspension (Sottolichio and Castaing, 1999;
558 Etcheber et al., 2007; Savoye et al., 2012). These characteristics account for the higher

559 bacterial contribution in this system. Regarding OM quality, the higher occurrence of
560 bacteria in relation with continental degraded POM has been reported in other studies
561 using different biomarkers in both marine (Berto et al., 2013; Lowe et al., 2014) and
562 estuarine (Bourgoin and Tremblay, 2010; Savoye et al., 2012) systems. Correlatives
563 approaches have been tested to characterize this relationship and clearly demonstrate
564 this link with degraded POM (Lowe et al., 2014) or to link bacterial production with
565 material ongoing degradation processes (Crump et al., 2017), both studies taking into
566 account for system peculiarities.

567 The inverse relationship observed between bacterial contribution and primary
568 producers in systems impacted by seasonality (i.e. Arcachon lagoon, bay of Banyuls and
569 pk86) reflects a switch in basal productivity: autotrophic spring and summer
570 production provides most of the energy fuelling higher levels in the food webs, whereas
571 winter period is likely associated the recycling of OM and high remineralisation due to
572 heterotrophic activity (i.e. more bacteria). Conversely, in highly turbid systems
573 dominated by refractory material such as the Gironde estuary, productivity is low and
574 the balance of the ecosystem is in favour of heterotrophic processes (Abril et al., 2002).
575 Terrestrial detritus has a low bioavailability for consumers, nevertheless, particle-
576 attached bacteria acts as a central component for detrital food webs (Crump et al.,
577 1998). Its high contribution to POM in the Gironde estuary makes the refractory
578 material available as a possible food source for consumers at higher trophic levels
579 (David et al., 2016). This has to be considered in carbon budgets.

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

593 Difficulties mainly rise up from the fact that POM is already a mix of different sources
594 (i.e. need to identify each source and its signature) where bacteria are attached to
595 particles, leading to 1) difficulties in isolating bacterial cells from the POM matrix and to
596 2) identify its specific signature. In a study from Hansman and Sessions, (2015), $\delta^{13}\text{C}$
597 isotopic signature of different phytoplankton cells populations (e.g. Synechococcus,
598 Diatoms) of *in situ* samples were determined by coupling fluorescence-activated cell
599 sorting with a specialized micro-combustion interface and isotope-ratio mass

600 spectrometry. This method could be applied to isolate bacterial cells and measure its
601 isotopic signature. However, the authors raise few technical difficulties regarding the
602 application of the method on the bacterial compartment. First, there is a necessity of
603 adapting protocols (i.e. isolate bacteria from their substrate, pre-concentration) to get
604 enough material of the targeted cell population for isotopic analyses. Second, as the cell
605 sorting method is based on optical and fluorescence properties of the cells, labelling
606 heterotrophic cells is required, being however aware of the possible impact of adding a
607 carbon from a probe (i.e. LysoTracker Green or specific oligonucleotide FISH probes) on
608 isotopic signature. Nevertheless, this approach remains very promising.

609 **5. Conclusion**

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

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

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

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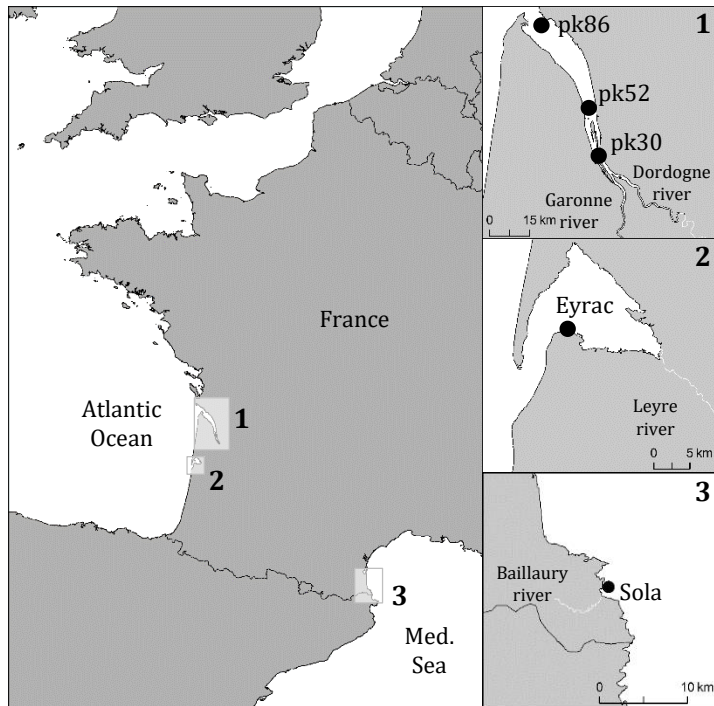


Figure 1: Studied systems and stations: 1. Gironde Estuary (3 stations: pk30, pk52 and pk86), 2. Arcachon Lagoon (Eyrac), 3. Bay of Banyuls (Sola) and their respective rivers. Med. Sea: Mediterranean Sea.

Source/station		Pelagic PP			Continental		Benthic PP		
		Phyto.	Diazo.	River.	Labile terr.	Refract. terr.	Macroalg.	Seagrasses	MPB
Arcachon lagoon	$\delta^{15}\text{N}$	5.2±1.2*	-	3.8±0.9*	-	-	9.8±1.6	6.6±1.2	4.0±0.6
	$\delta^{13}\text{C}$	-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	$\delta^{15}\text{N}$	4.0±1.2	-1.2±0.9	5.2±1.0*	-	-	-	-	-
	$\delta^{13}\text{C}$	-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	$\delta^{15}\text{N}$	-	-	-	-	-	-	-	-
	$\delta^{13}\text{C}$	-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.

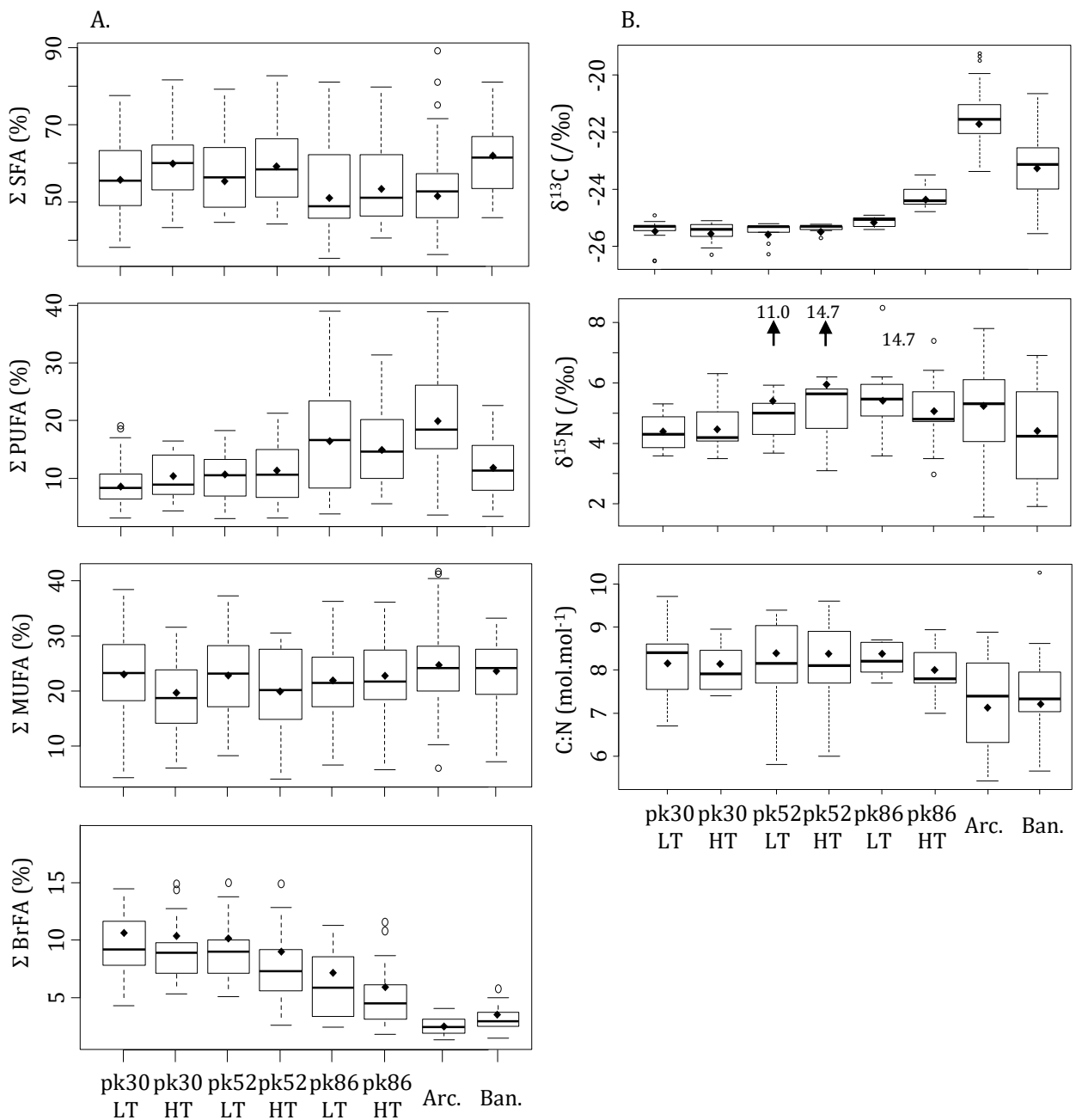


Figure 2: Boxplots for the 8 studied stations and tides over the entire annual cycle A. on FA classes in % of contribution to the total FA (left panel), B. on elemental and isotopic ratios of carbon and nitrogen ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C:N) (right panel). SFA: saturated, MUFA: 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.

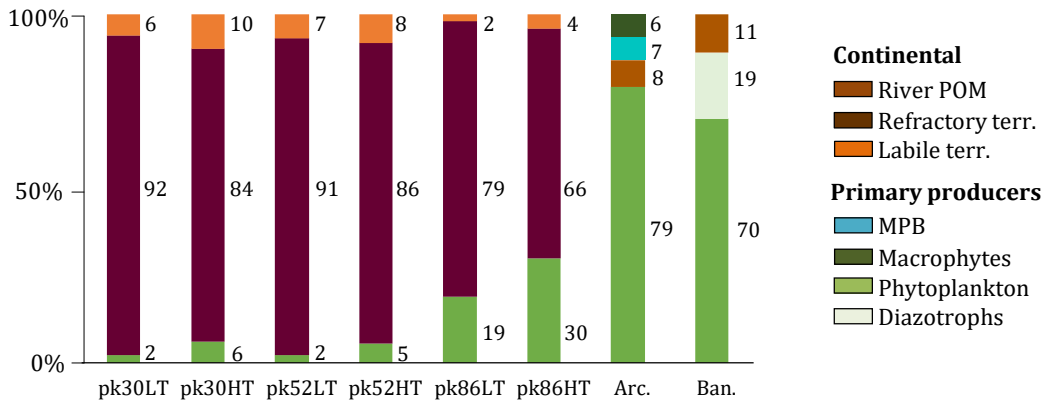


Figure 3: Mixing model outputs. Proportions of contribution of each source to the POM pool. Absolute uncertainty associated to the mixing-model outputs was usually close to 10%. Arc.: Arcachon lagoon. Ban.: bay of Banyuls. LT: low tide. HT: high tide. MPB: microphytobenthos

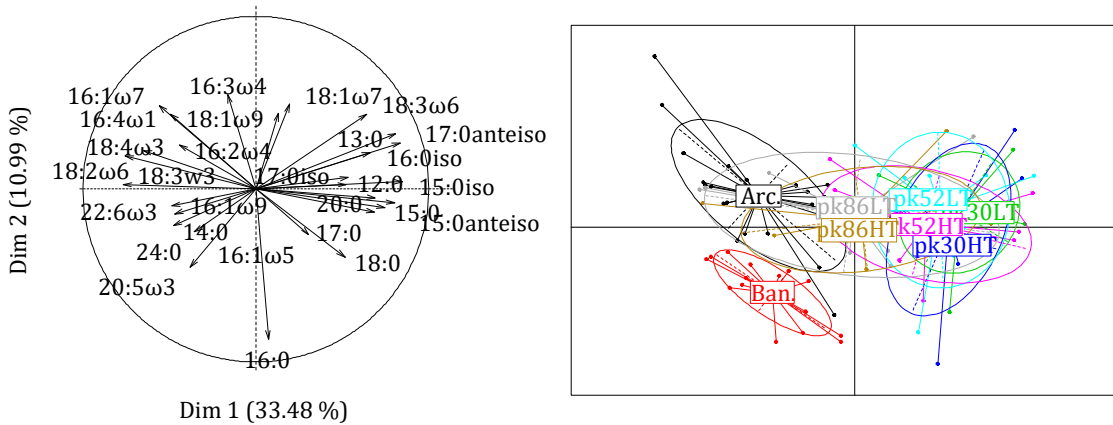


Figure 4: Principal component analysis (PCA) performed on FA data. Left panel: variables (individual FA), right panel: individual samples grouped by station. Arc.: Arcachon lagoon. Ban.: bay of Banyuls. HT: high tide. LT: low tide.

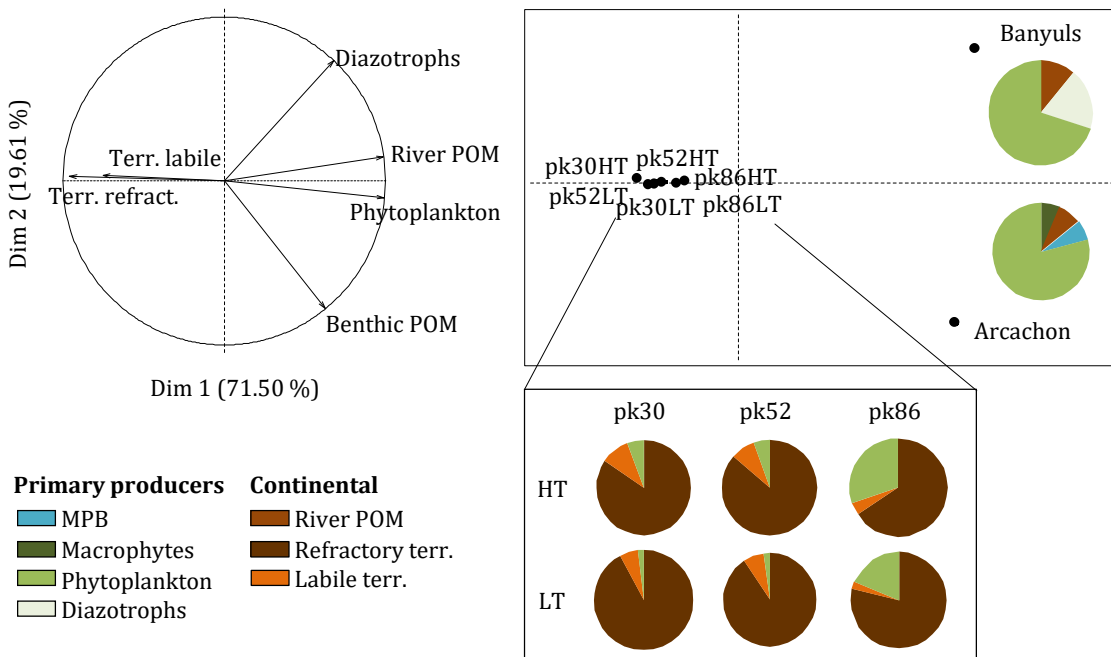


Figure 5: Principal component analysis (PCA) performed on POM composition proportions data computed by mixing models on isotopic data. Left panel: variables (sources of POM), right panel: the stations. Diagrams illustrate POM composition for each station showing mean annual percentage of each source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

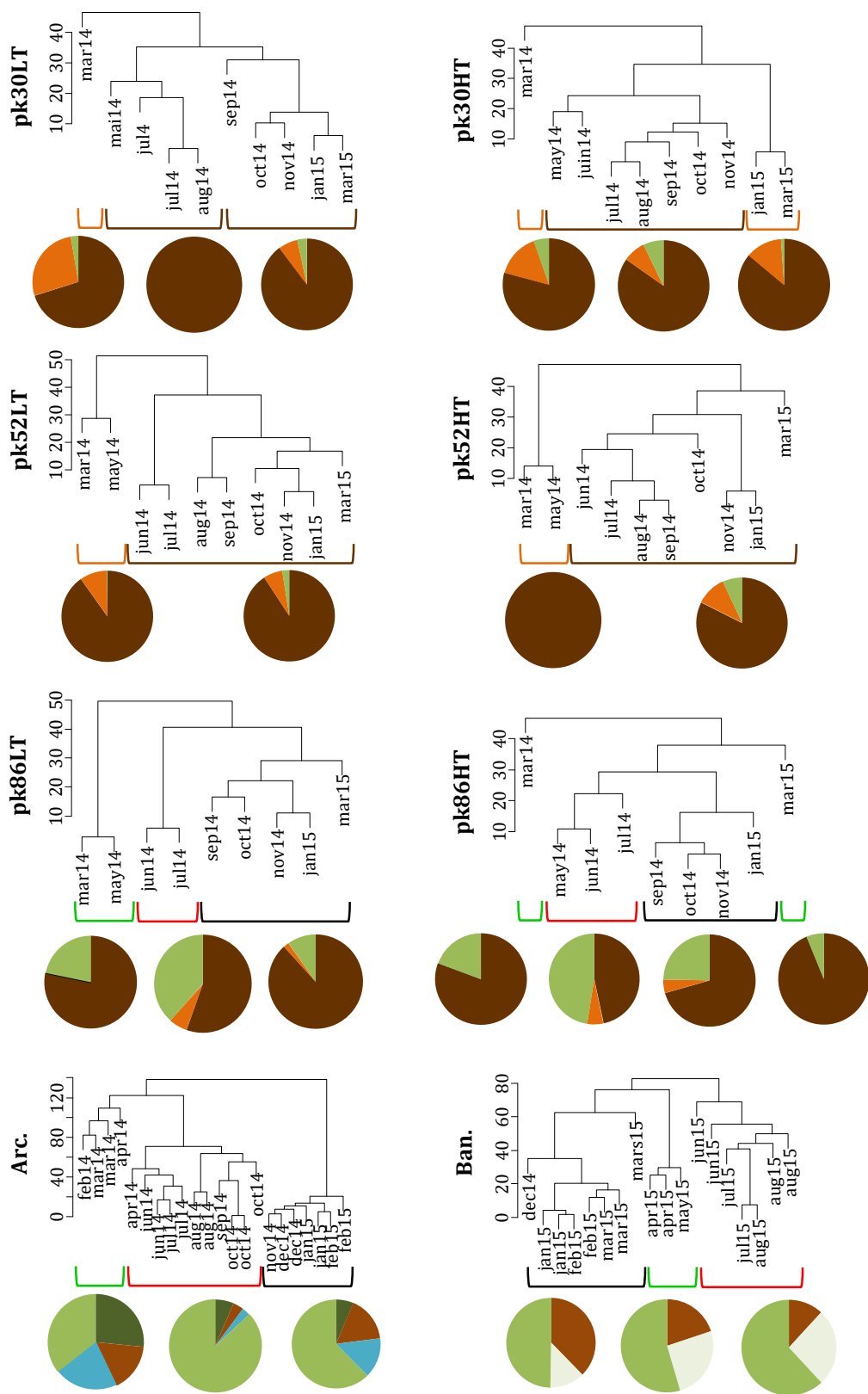


Figure 6: Constraint agglomerative hierarchical classification defining periods based on FA profiles. Pie charts illustrate POM composition (mixing models outputs) mean percentage of each source over each period. Arc.: Arcachon lagoon. Ban.: bay of Banyuls. HT: high tide: LT: low tide. For pie chart 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.

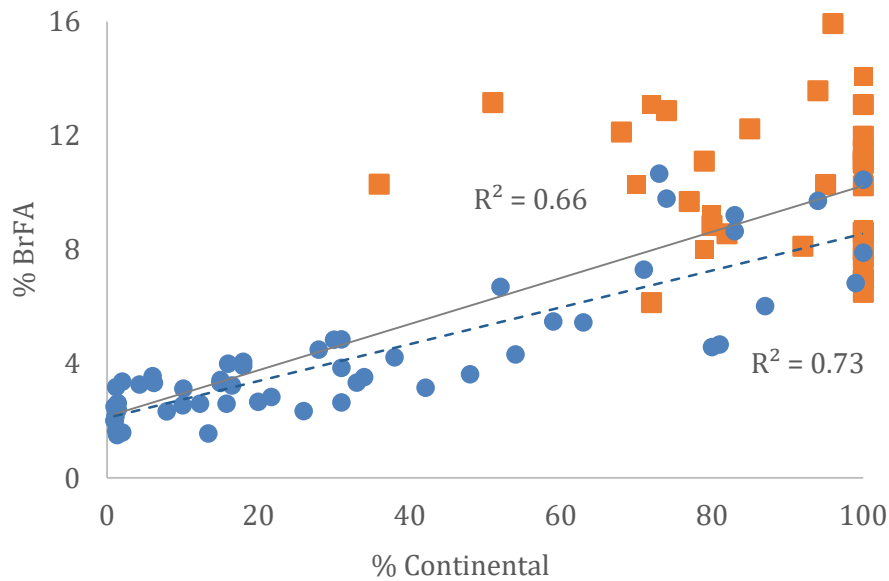


Figure 7: relationship between the % of bacterial FA markers (BrFA) of TFA and the % of Continental POM (i.e. refractory terrestrial or river POM) for all sampling dates of all stations ($R^2_{adj.}=0.66$, grey full line), all marine stations (blue circles, Arcachon lagoon, bay of Banyuls and pk86 HT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