



Spatio-temporal variation of suspended and sedimentary organic matter quality in the Bay of Marseilles (NW Mediterranean) assessed by biochemical and isotopic analyses

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ABSTRACT

Isotopic and biochemical features of suspended particulate organic matter (POM) in the water column and of sedimentary organic matter (SOM) were investigated seasonally in the Bay of Marseilles. Biochemical compounds (carbohydrates, lipids and proteins) were consistently more concentrated in POM than in SOM, with SOM mainly composed of insoluble carbohydrates. POM displayed lower $\delta^{13}\text{C}$ and higher $\delta^{15}\text{N}$ values than SOM. Phytoplanktonic production represented the major contributor of POM year-round with spatial and seasonal variations. Climatic parameters and wind-induced currents created differences in POM contributions, with more important inputs of terrestrial OM at one sampling site. Spatial and seasonal variations were lower for SOM. The composition of this pool appeared to be linked with the permanent inputs of phytoplankton and *Posidonia oceanica* detritus. The combined use of biochemical and isotopic analyses was a useful tool to characterize OM pools and would help understanding the trophic functioning of this coastal environment.

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1. Introduction

Coastal ecosystems represent one of the most productive systems on Earth (Duarte and Cebrián, 1996). Positioned at the interface between terrestrial and open sea ecosystems, coastal zones are under the influence of different sources of organic matter (OM) (Bode et al., 2006). Phytoplanktonic production is generally the main source of carbon in these zones, but local benthic production also represents a non-negligible contributor to organic matter pools, as do inputs of terrestrial matter carried by coastal rivers (Riera and Richard, 1996; Darnaude et al., 2004). All these inputs supply two complex and heterogeneous pools of organic matter, the suspended particulate organic matter pool (POM) in the water column and the sedimentary organic matter pool (SOM) which fuel the coastal food webs (Savoye et al., 2003; Tesi et al., 2007). POM is actually a mixture of living and detrital material, including bacteria, fecal pellets, dead zooplanktonic cells and detritus (Harmelin-Vivien et al., 2008; Frangoulis et al., 2011). SOM is considered to be mainly a detrital pool which is fueled by dead material from benthic and pelagic marine producers (Holmer et al., 2004; Papadimitriou et al., 2005) and from riverine inputs, but it could also result from important local microphytobenthic production (Barranguet et al., 1996). This multiplicity of sources

has always made it difficult to understand the relative influence of each source on these pools and its use by consumers.

Analysis of stable isotopes has been used successfully to solve this problem (Maksymowska et al., 2000; Bode et al., 2006). This method is based on the natural coexistence of light and heavy stable isotopes with defined proportions which are modified by biochemical processes. As terrestrial and marine primary producers use different photosynthetic pathways, they discriminate differentially between light and heavy isotopes, and have different isotopic ratios of carbon and nitrogen (Peterson and Fry, 1987). Organic matter from land plants is commonly considered to be highly ^{13}C depleted and to display values lower than -28‰ (Riera and Richard, 1996). As coastal rivers carry this matter, riverine POM displays similar low values (Banaru et al., 2007; Tesi et al., 2007; Harmelin-Vivien et al., 2010). The $\delta^{13}\text{C}$ values of marine benthic producers may be highly variable, with some red algae displaying values lower than -30‰ (Pinnegar and Polunin, 2000) and seagrasses, which are enriched in ^{13}C , reaching isotopic ratios close to -10‰ (Hemminga and Matteo, 1996). Isotopic signatures of marine phytoplankton are considered to be close to -22‰ in temperate waters (Fry and Wainright, 1991; Harmelin-Vivien et al., 2008). The isotopic ratios of OM pools will thus be representative of the relative influence of each of these sources.

Biochemical analyses of OM pools may also be a useful tool for assessing their origin. OM is usually divided into labile and refractory matter. Labile matter is composed of hydrosoluble compounds readily metabolically available for consumers (Danovaro et al.,

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2000), such as proteins, lipids and simple carbohydrates whereas refractory matter contains more complex compounds, such as structural carbohydrates or fulvic acids and need bacterial transformation before its consumption (Danovaro et al., 2001). In marine coastal environments, labile dissolved OM is usually composed by phytoplanktonic production and refractory OM is brought to sea by terrestrial inputs (Amon and Benner, 1996). Traditional conception considers that low-molecular weight compounds are generally main components of labile matter and much complex compounds, like heteropolysaccharides, represent refractory matter. But this size reactivity continuum is getting more complex by diagenetic degradation processes which could result in low molecular weight refractory compounds (Amon and Benner, 1996). A high concentration of refractory compounds in a pool clearly indicates a detritic origin, whereas a high concentration of labile compounds indicates a recently synthesized OM. A complementary approach is based on the use of the carbon/nitrogen (C/N) ratio to determine OM quality. Since proteins are the main N compounds in OM, low C/N values indicate an important quantity of amino acids and consequently an OM of high nutritional quality (Danovaro et al., 2001).

POM and SOM, through their consumption by suspensivores and detritivores, are considered the major energy inputs driving the dynamics of the benthic communities (Pfannkuche, 1993; Salen-Picard et al., 2002). The knowledge of the nature, origin and variation of POM and SOM is a prerequisite for future determination of the use and transfer of OM in coastal trophic webs. Numerous studies on isotopic or biochemical composition of POM or SOM were performed in different locations of the Mediterranean Sea such as coastal lagoons (Vizzini and Mazzola, 2003; Covazzi Harriague et al., 2007), estuarine zones (Darnaude et al., 2004; Harmelin-Vivien et al., 2008) or underwater caves (Fichez, 1991; Rastorgueff et al., 2011) but not on rocky coastal zones as in the present study. Moreover none of them combine the analysis of stable isotopes and biochemical composition of these pools and looked for their seasonal variability. The aims of the present study were thus (a) to determine the main isotopic and biochemical features of the two OM pools, (b) to assess their spatial and seasonal

variations and (c) to link these variations with influences of allochthonous sources of OM under the control of climatic and hydrologic parameters.

2. Materials and methods

2.1. Study site

The Bay of Marseilles is divided in two parts. The northern part is the bigger and deeper (mean depth 52 m) of the two and includes the commercial harbor facilities and industrial activities. The southern part is shallower (mean depth 30 m) and has no industry. Two sampling sites were chosen in the south of the Bay due to their proximity to potential sources of OM (Fig. 1). The southern site (V6) is close to the *Posidonia oceanica* (Linnaeus) De-lile meadow and to the mouth of the Huveaune River. The river flow is deflected to the Marseilles sewage outfall most of the time, but after heavy rain events it flows briefly to the sea through its natural bed. The northern site (V3) is further from these potential sources of organic matter and closer to the northern part of the Bay. Both sites are at depths of 30 m with similar sandy bottom with dead matte of *P. oceanica* (underlying structure of *P. oceanica* meadows constituted of rhizomes and roots intermingled with sediments).

Sampling was performed once per season in spring, summer, autumn and winter 2010. Subsurface seawater was sampled above each site. Water sampling was performed four times in the Huveaune River during flow periods. Huveaune samplings coincided with the four main rain events in Marseilles in 2010 (Météo France, data not shown). All water samples were prefiltered on a 200 µm mesh-sieve to remove large detritus. Marine and riverine POM were obtained by filtering water on pre-weighed Whatman GF/F filters precombusted for 4 h at 500 °C to remove any trace of organic matter. Filters were then dried, weighed again to obtain dry weight and kept in a dry and dark place before stable isotope and biochemical analyses. A total of 15 filters was obtained at each season. Additional data on isotopic values of POM in the vicinity of the

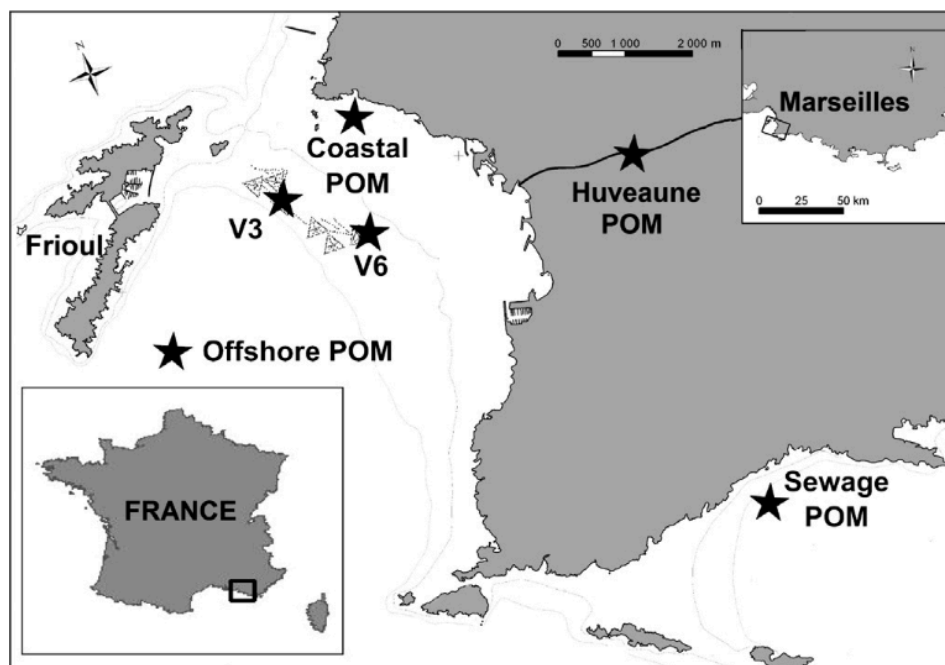


Fig. 1. Location of sampling sites (V3 and V6) and of POM additional sampling sites in the Bay of Marseilles.

sampling area were obtained from previous studies (Sewage POM: Marseilles sewage outfall (Topçu et al., 2010), Offshore POM: water outside of the Bay of Marseilles and away from urban influence (Darnaude et al., 2004), Coastal POM: coastal water POM under urban influence (M. Harmelin-Vivien, unpubl. data)). Sediment samples were collected by SCUBA diving at each season on each site. The sediment surface layer was sampled at three stations at each site. An additional sediment sampling was performed in the *P. oceanica* meadow near V6 site. Sediment samples were stored frozen and were freeze-dried before analysis.

2.2. Stable isotope analysis

SOM samples were ground into a fine powder using an agate mortar and pestle. As SOM and POM contain carbonates, an acidification step was necessary to remove ^{13}C -enriched carbonates. SOM and filter materials were split in half. One part received 1% HCl treatment before rinsing and drying, and was used for $\delta^{13}\text{C}$ analyses. The other part did not receive further treatment and was used for $\delta^{15}\text{N}$ analyses. POM was collected by scraping the surface of acidified and non acidified filters. For each site and season, three replicates were done on POM and 27 on SOM for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Stable isotope measurements were performed with a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Bremen, Germany) coupled to an elemental analyzer (Flash EA1112 Thermo Scientific, Milan, Italy). Results are expressed in δ notation relative to Pee Dee Belemnite and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, according to the equation $\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 10^3$, where X is ^{13}C or ^{15}N and R is the isotope ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. For both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, measurement precision is $<0.1\text{‰}$ (replicate measurements of internal laboratory standards, acetanilide). Percentage of organic C and organic N were obtained using the elemental analyzer and were used to calculate the sample C/N ratio.

2.3. Biochemical analyses

Determination of biochemical concentrations were performed on SOM and POM to assess the composition of OM pools. Soluble and insoluble carbohydrates, lipids and proteins were determined by spectrophotometric methods. Soluble carbohydrates were extracted from SOM and POM with distilled water (100 °C, 20 min) and insoluble carbohydrates were extracted in the residue. Both soluble and insoluble carbohydrates concentrations were determined after Dubois et al. (1956) and were expressed as glucose equivalents. Lipids concentrations were determined following Bligh and Dyer (1959) and were expressed as tripalmitic acid equivalent. Proteins concentrations were determined according to Lowry et al. (1951) and were expressed as bovine sero-albumin equivalent. All analyses were run on triplicates. For each compound at each site and season, 9 analyses were performed on POM and 27 on SOM. To allow comparisons between POM and SOM, all biochemical concentrations were in $\mu\text{g mg}^{-1}$. For sedimentary organic matter, the concentration measured by spectrophotometry is calculated against the weight of sediment used for the analysis. For POM, the concentration measured is calculated against the weight of the dry matter retained on each filter.

2.4. Mixing models

As POM and SOM are mixed pools under the influence of different sources of OM, mixing models were used to assess the relative contributions of each of these sources on the global pools at each location. Contributions were calculated using IsoSource software

(Phillips and Gregg, 2003). For POM, available data on isotopic values of POM in the vicinity of the sampling zone (coastal, offshore, Huveaune River and sewage outfall POM) were computed to calculate the mean annual contribution of these sources to V3 and V6 POM. As SOM may also receive inputs from seagrasses, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values representative of *P. oceanica* were added to POM values for the calculation of SOM mean contributors. *P. oceanica* values were calculated from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean value measurements of living and dead leaves sampled throughout the year in the seagrass meadow near V6 (P. Cresson, unpubl. data). Mean calculated values were -15.46‰ for $\delta^{13}\text{C}$ and 4.16‰ for $\delta^{15}\text{N}$. The range of probable contributions was calculated using 1% increments and a tolerance of 0.1.

2.5. Statistical analyses

After testing for normality (Kolmogorov-Smirnoff test) and homogeneity of variances (Levene test), two way ANOVA were performed to assess the effect of time (season) and space (location) on isotopic ratios and biochemical concentrations. Post-hoc comparisons of means were performed with Student–Newman–Keuls tests. When assumptions of homogeneity of variances or normality were not reached, non-parametric Kruskal–Wallis ANOVAs were performed followed by post hoc non-parametric paired comparison tests. All statistical analyses were done with Statistica® 9.1 software.

3. Results

3.1. Variations of biochemical composition of organic matter pools

Biochemical concentrations were consistently higher in POM than in SOM for all the parameters analyzed (Table 1). Insoluble carbohydrates represented the main compounds of SOM (nearly 65% of the total amount of biochemical compounds) whereas no clear predominance appeared for POM, with insoluble carbohydrates, lipids and proteins displaying similar mean concentrations. Important seasonal variations were observed in POM (Table 2). Concentrations were significantly higher in summer for all parameters with the exception of soluble carbohydrates (Fig. 2). Concentrations were lowest in autumn and intermediate in winter and spring. Spatial variations were also evidenced in POM, with higher lipid and protein concentrations in V6 than V3 (Table 2) and explained high variability observed for seasonal concentrations. SOM appeared to be less variable than POM, even if small differences were noted. A decrease in all biochemical parameters appeared in spring (Fig. 3), while no real difference was observed for the other three seasons. Concentrations in SOM were significantly higher at V6 than at V3 for insoluble carbohydrates, soluble carbohydrates, and proteins, but not for lipids (Table 2).

3.2. Stable isotope ratios of organic matter pools

Differences were observed between SOM and POM stable isotope ratios (Table 1). $\delta^{13}\text{C}$ values were higher for SOM and $\delta^{15}\text{N}$ values were higher for POM. C/N ratio also showed substantial differences, with lower values for POM than for SOM. Spatial differences existed for $\delta^{13}\text{C}$ between V3 and V6 (Fig. 4). V6 POM displayed lower values than V3. This low value appeared similar to values observed for POM from terrestrial origin (sewage, outfall and Huveaune). On the contrary, the higher $\delta^{13}\text{C}$ value obtained in V3 POM was intermediate between values measured for coastal and offshore stations. Applying the IsoSource mixing model to stable isotopes ratios of POM suggested different contributions of OM sources for the two sampling sites (Fig. 5). Huveaune and coastal

Table 1

Mean values ($\pm$ standard deviation) in POM and SOM of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C/N ratio, concentrations of insoluble carbohydrates (IC), soluble carbohydrates (SC), lipids and proteins, and results of Mann–Whitney mean comparison tests.

	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C/N	IC ($\mu\text{g mg}^{-1}$)	SC ($\mu\text{g mg}^{-1}$)	Lipids ($\mu\text{g mg}^{-1}$)	Proteins ($\mu\text{g mg}^{-1}$)
POM	-24.18 ± 0.85	5.13 ± 0.90	6.33 ± 1.13	11.65 ± 10.14	2.66 ± 1.61	8.70 ± 5.85	9.81 ± 12.91
SOM	-21.95 ± 0.57	3.67 ± 0.25	13.05 ± 2.06	3.91 ± 1.52	0.47 ± 0.36	0.81 ± 0.24	0.95 ± 0.54
Statistics	$Z = 7.9$ $p < 0.001$	$Z = 6.9$ $p < 0.001$	$Z = 8.0$ $p < 0.001$	$Z = 5.4$ $p < 0.001$	$Z = 5.6$ $p < 0.001$	$Z = 8.0$ $p < 0.001$	$Z = 5.1$ $p < 0.001$

Table 2

Variation of the isotopic and biochemical parameters measured in POM and SOM. Letters stand for the statistical test used (Z: Mann–Whitney; F: two way ANOVA; H: non parametric Kruskal Wallis ANOVA). IC Insoluble Carbohydrate, SC soluble carbohydrates, Sp spring, Su summer, Au autumn, Wi Winter.

Parameter	Factor	Statistics	p		Post-hoc
POM					
$\delta^{13}\text{C}$ (‰)	Site	$F = 91.03$	<0.001	***	V3 > V6
	Season	$F = 33.60$	<0.001	***	Sp < Wi = Au = Su
	Site $\times$ season	$F = 7.17$	<0.001	***	
$\delta^{15}\text{N}$ (‰)	Site	$F = 1.83$	0.19	n.s.	
	Season	$F = 11.81$	<0.001	***	Sp < Au < Su = Wi
	Site $\times$ season	$F = 0.23$	0.87	n.s.	
C/N	Site	$F = 9.76$	0.01	*	V3 < V6
	Season	$F = 12.65$	<0.001	***	Sp = Su < Au = Wi
	Site $\times$ season	$F = 4.09$	0.02	*	
IC ($\mu\text{g mg}^{-1}$)	Site	$Z = 1.69$	0.09	n.s.	
	Season	$H = 15.65$	0.001	***	Au = Wi < Sp < Su
	Site $\times$ season	$H = 20.90$	0.003	**	
SC ($\mu\text{g mg}^{-1}$)	Site	$F = 0.52$	0.48	n.s.	
	Season	$F = 13.49$	<0.001	***	Su = Au = Wi < Sp
	Site $\times$ season	$F = 3.11$	0.06	n.s.	
Lipids ($\mu\text{g mg}^{-1}$)	Site	$F = 9.88$	0.01	**	V3 < V6
	Season	$F = 11.28$	<0.001	***	Sp = Au = Wi < Su
	Site $\times$ season	$F = 0.50$	0.69	n.s.	
Proteins ($\mu\text{g mg}^{-1}$)	Site	$F = 6.50$	0.02	*	V3 < V6
	Season	$F = 82.10$	<0.001	***	Au < Sp < Wi < Su
	Site $\times$ season	$F = 56.28$	<0.001	***	
SOM					
$\delta^{13}\text{C}$ (‰)	Site	$F = 105.77$	<0.001	***	V3 < V6
	Season	$F = 15.70$	<0.001	***	Sp = Su > Wi = Au
	Site $\times$ season	$F = 1.65$	0.18	n.s.	
$\delta^{15}\text{N}$ (‰)	Site	$F = 38.73$	<0.001	***	V3 < V6
	Season	$F = 0.88$	0.45	n.s.	
	Site $\times$ season	$F = 5.63$	<0.001	***	
C/N	Site	$F = 37.46$	<0.001	***	V3 > V6
	Season	$F = 33.87$	<0.001	***	Sp < Su < Au = Wi
	Site $\times$ season	$F = 5.33$	<0.001	***	
IC ($\mu\text{g mg}^{-1}$)	Site	$Z = -2.98$	0.003	**	V3 < V6
	Season	$H = 50.00$	<0.001	***	Sp < Su = Au = Wi
	Site $\times$ season	$H = 68.87$	<0.001	***	
SC ($\mu\text{g mg}^{-1}$)	Site	$Z = -3.90$	<0.001	***	V3 < V6
	Season	$H = 67.00$	<0.001	***	Wi = Su < Au = Sp
	Site $\times$ season	$H = 118.35$	<0.001	***	
Lipids ($\mu\text{g mg}^{-1}$)	Site	$Z = -1.37$	0.17	n.s.	
	Season	$H = 20.56$	<0.001	***	Sp < Su = Wi = Au
	Site $\times$ season	$H = 41.57$	<0.001	***	
Proteins ($\mu\text{g mg}^{-1}$)	Site	$Z = -2.40$	0.02	*	V3 < V6
	Season	$H = 95.16$	<0.001	***	Sp < Au = Wi < Su
	Site $\times$ season	$H = 129.20$	<0.001	***	

n.s. not significant.

Post-hoc post hoc comparison of means (Student–Newman–Keuls or paired comparison test).

* Significant at $p < 0.05$.

** Significant at $p < 0.01$.

*** Significant at $p < 0.001$.

POM were the main contributors of V6 POM (mean contribution of 36% and 38% respectively) whereas V3 POM was more influenced by coastal and offshore POM (50% and 37% respectively). High seasonal variations were evidenced for POM. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values

were low in spring, reached a maximum in summer, and were intermediate in autumn and winter (Table 3). The substantial standard deviations observed for $\delta^{13}\text{C}$ in summer, autumn and winter were due to important differences between sites (Fig. 6). Isotopic

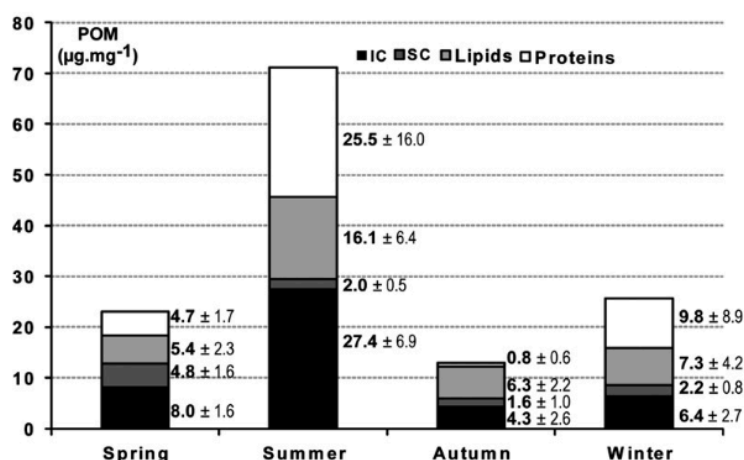


Fig. 2. Seasonal variations of mean concentrations (± standard deviation) of Insoluble Carbohydrates (IC), Soluble Carbohydrates (SC), Lipids and Proteins measured in POM.

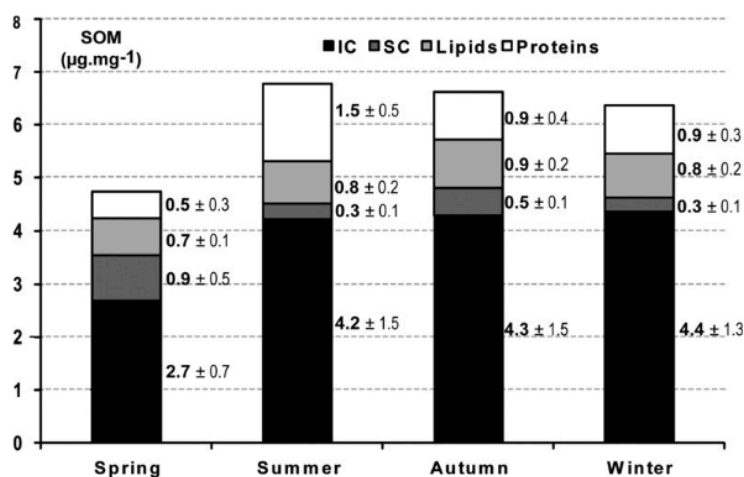


Fig. 3. Seasonal variations of mean concentrations (± standard deviation) of Insoluble Carbohydrates (IC), Soluble Carbohydrates (SC), Lipids and Proteins measured in SOM.

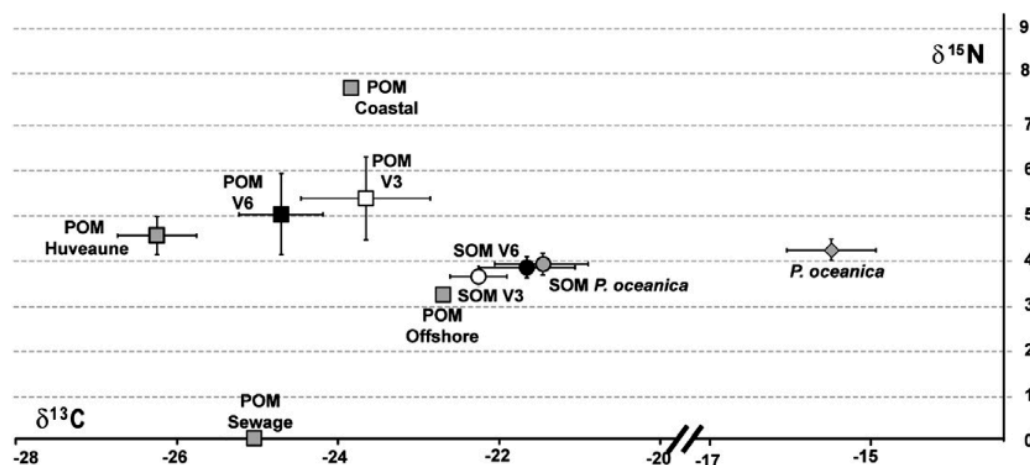


Fig. 4. Spatial variation of POM (squares) and SOM (circles) isotopic (δ¹³C and δ¹⁵N) ratios at V3 (black) and V6 (white). Additional data on potential sources of organic matter (grey) result from this work (Huveaune, sediment from *P. oceanica* meadow, mean *P. oceanica* dead and living leaves) or from previous studies (sewage, Topçu et al., 2010, coastal, M. Harmelin-Vivien unpubl. data, offshore, Darnaude et al., 2004). For graphic convenience, the δ¹³C axis was broken between -22‰ and -17‰.

ratios measured in SOM showed low spatial and temporal variations. Values were significantly higher at V6 than at V3 and were closer to ratios measured for *P. oceanica* meadow SOM. Mixing

models showed that SOM was under the influence of two main contributors, offshore POM and *P. oceanica*. Offshore POM contributed to SOM with values close to 30% at both sites (32% for V3 and

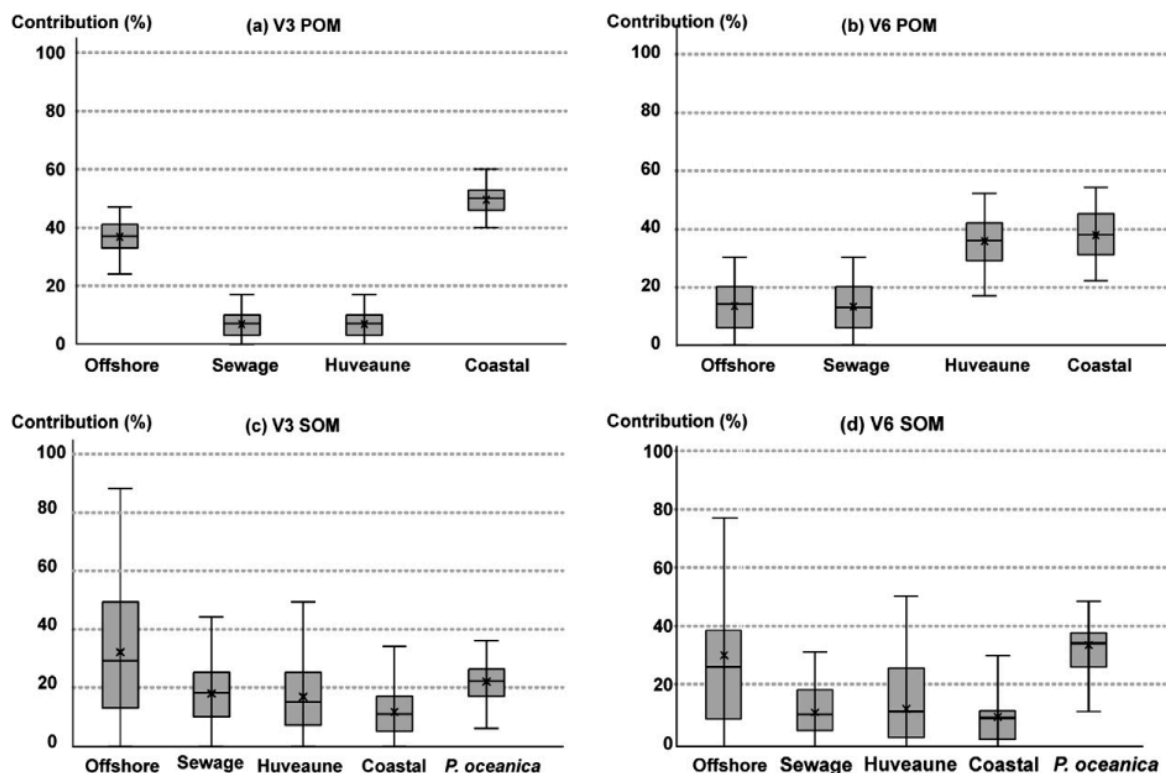


Fig. 5. Contributions of offshore, sewage, Huveaune and coastal POM to water POM at V3 (a) and V6 (b) and contributions of these sources plus *P. oceanica* leaves to SOM at V3 (c) and V6 (d), calculated with IsoSource software. Bottoms and tops of the boxes indicate lower and upper quartiles, horizontal bands represent medians, crosses indicate means and ends of whiskers represent minimal and maximal values.

Table 3

Seasonal means ($\pm$ standard deviation) of stable isotope values and C/N ratios of POM ($n = 6$) and SOM ($n = 27$).

		$\delta^{13}\text{C}$	SD	$\delta^{15}\text{N}$	SD	C/N	SD
POM	Spring	-25.02	0.23	3.89	0.29	5.64	0.44
	Summer	-23.59	0.58	5.80	0.40	5.95	0.82
	Autumn	-23.78	1.05	5.00	0.50	5.80	1.62
	Winter	-24.33	0.63	5.83	0.50	6.45	0.75
SOM	Spring	-21.84	0.60	3.62	0.27	11.32	1.68
	Summer	-21.73	0.52	3.66	0.24	13.01	1.36
	Autumn	-22.20	0.60	3.70	0.29	13.72	2.20
	Winter	-22.08	0.44	3.68	0.20	14.17	1.73

28% for V6). IsoSource values also showed a fairly similar contribution of *P. oceanica* inputs, with higher values at V6 (29% at V6 and 22% at V3). *P. oceanica* was the only source of OM with no null contribution value on SOM. Seasonal variation of SOM appeared only for $\delta^{13}\text{C}$ in two groups, spring and summer with higher values, and winter and autumn with lower values. No linear relationship was observed between lipids concentrations and $\delta^{13}\text{C}$ either in POM (Lipids = $21.28 + 0.52 \times \delta^{13}\text{C}_{\text{POM}}$, $r^2 = 0.006$, $p > 0.05$) or in SOM (Lipids = $-0.07 - 0.04 \times \delta^{13}\text{C}_{\text{SOM}}$, $r^2 = 0.008$, $p > 0.05$).

4. Discussion

4.1. Origin of the organic matter

The particulate organic matter in seawater and sediment in coastal zones are heterogeneous pools composed of a mixture of living matter phytoplankton and zooplankton in the water column, and phytobenthos and meiofauna in the sediment, but also of detrital matter from marine or terrestrial origin. In marine animals,

a linear correlation between $\delta^{13}\text{C}$ and lipids is commonly observed, due to low $\delta^{13}\text{C}$ values of lipids (Sweeting et al., 2006). The absence of any correlation between lipids and $\delta^{13}\text{C}$ in POM and SOM was linked to their heterogeneous composition. Variations of the relative importance of each source of matter will modify the global composition of OM pools, which may be determined through their biochemical and isotopic signatures.

In temperate waters, phytoplankton commonly display $\delta^{13}\text{C}$ values comprised between -22‰ and -20‰ (Fry and Wainright, 1991; Harmelin-Vivien et al., 2008). $\delta^{13}\text{C}$ mean value measured for POM in the Bay of Marseilles in the present study ($-24.18 \pm 0.85\text{‰}$) was lower than usual values. Low values of marine POM $\delta^{13}\text{C}$ are commonly interpreted as the reflect of substantial contribution of terrestrial OM on POM (Riera and Richard, 1996; Harmelin-Vivien et al., 2008). But similar low $\delta^{13}\text{C}$ values have already been measured in local coastal phytoplankton samples (Rastorgueff et al., 2011). The C/N ratio close to 6 for POM in the present study was coherent with values reported for phytoplanktonic cells for which C/N ratios usually range between 6 and 10

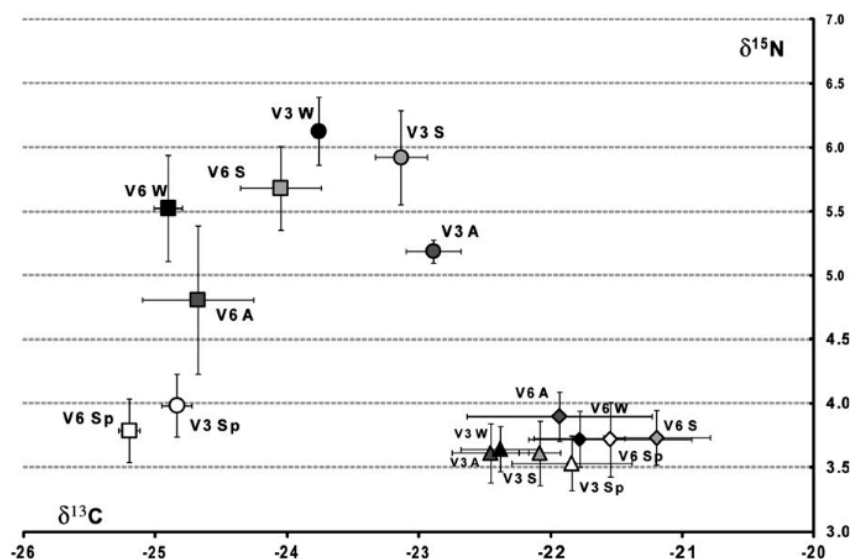


Fig. 6. Spatio-temporal variation of isotopic ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of POM and SOM on each sampling site and season. V3 POM: circles; V6 POM: squares; V3 SOM: triangles; V6 SOM: diamonds. Sp: spring (white); S: summer (light grey); A: autumn (dark grey); W: winter (black).

(Biddanda and Benner, 1997; Savoye et al., 2003). POM also displayed high lipid and protein concentrations. When POM biochemical concentrations and phytoplankton counting are performed on the same samples, increases in proteins and lipids, the main constituents of phytoplanktonic cells (Handa, 1969), always occur simultaneously with phytoplankton blooms (Puscedu et al., 1996; Covazzi Harriague et al., 2007). Our results indicated the major role of phytoplanktonic production in the marine POM of the Bay of Marseilles and were coherent with previous studies which reported mean annual phytoplanktonic production of $88 \text{ gC m}^{-2} \text{ a}^{-1}$ (Lefèvre et al., 1997).

SOM differed from POM in both its isotopic and its biochemical characteristics. In coastal ecosystems under the influence of large rivers, low or non-significant differences between POM and SOM $\delta^{13}\text{C}$ could be evidenced, due to a predominant contribution of terrestrial matter on deltaic SOM (Banaru et al., 2007). In the Bay of Marseilles, differences between POM and SOM and the higher $\delta^{13}\text{C}$ values observed in SOM rule out a major influence of riverine matter on sediment. SOM isotopic signatures appeared to be driven by the proximity of a *P. oceanica* meadow which provided large amounts of detritus. The organic matter produced by this seagrass is mainly composed of high molecular weight compounds hard to degrade and which are sequestered in the sediment for long periods of time (Boudouresque et al., 2006). As seagrasses are known to present high $\delta^{13}\text{C}$ values ranging between -12‰ and -9‰ (Hemminga and Matteo, 1996), the high $\delta^{13}\text{C}$ values observed in SOM and the importance of insoluble carbohydrates may be linked with constant inputs of ^{13}C -enriched *P. oceanica* detrital matter. Mean contribution values calculated using mixing models for SOM contributors confirmed the importance of seagrass detritus at the two locations year-round, with a marked influence at V6, which is located close to seagrass meadows. Offshore POM also appeared to be an important contributor to SOM, as this matter is probably settling year-round, even if cautions must be taken due to high variability. A comparable pattern is observed in the Balearic Islands where sestonic particles and seagrass detritus are demonstrated to be the major contributors to SOM composition (Papadimitriou et al., 2005). The low contributions calculated for other POM (sewage, Huveaune and coastal) could be explained by occasional inputs, which were of little significance annually.

4.2. Seasonal variations of OM pools

Isotopic ratios and biochemical concentrations measured in POM were highly variable. Spring samples differed, with the lowest isotopic values and intermediate biochemical concentrations. The seasonal variation of phytoplanktonic communities may explain these variations. Grégori et al. (2001) evidence a massive bloom of picophytoplankton cells ($0.2\text{--}2 \mu\text{m}$) in spring in the Bay of Marseilles. In the Mediterranean Sea, the smallest phytoplanktonic cells ($<8 \mu\text{m}$) are markedly ^{13}C depleted in comparison to larger particles and display $\delta^{13}\text{C}$ values of between -25.4‰ and -22.5‰ (Rau et al., 1990). The low stable isotopes values of $\delta^{13}\text{C}$ recorded in spring may thus reflect the predominance of these small cells in the Bay of Marseilles. This explanation was supported by the conjunction of a high concentration of chlorophyll-*a* measured in the Bay (Table 4) with a low abundance of large phytoplanktonic cells (mainly diatoms and dinoflagellates) at the time of sampling (M. Golbol, pers. comm.). Winter POM was characterized by high $\delta^{15}\text{N}$ values and summer POM by both high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Abundance of phytoplankton cells is known to be important in summer in the Bay of Marseilles and some transient blooms can also appear in winter (Travers, 1971). Low concentrations of inorganic nutrients were also observed during these seasons (Table 4). The growth of phytoplanktonic cells on an impoverished pool of nitrates (where only ^{15}N enriched compounds remain) may be responsible for the high $\delta^{15}\text{N}$ values observed for POM in summer and winter, as described by Savoye et al. (2003) and Montoya (2007). Fry and Wainright (1991) also report a ^{13}C enrichment of phytoplankton at the end of a bloom. The high concentration of biochemical compounds in summer supported this hypothesis. Covazzi Harriague et al. (2007) show that phytoplankton is the main driver of seasonal fluctuations in POM quality and link high biochemical concentrations in water with high phytoplankton biomass. Rossi et al. (2003) report similar seasonal trends in biochemical concentrations of settling POM near Banyuls (west of the Gulf of Lions). They distinguish two periods, one spring – summer with biochemically enriched POM, and the other autumn – winter with impoverished POM. Finally, Puscedu et al. (1996) describe a comparable increase in protein concentration with diatom and dinobiont blooms in an Italian lagoon.

Table 4

Best available environmental data for the sampling zone at each season. Chl-a: mean concentration of chlorophyll a measured in surface water (data from A. Desnues – LOPB); NH_4^+ and NO_3^- : mean concentration of ammonium and nitrate measured in the Frioul SOMLIT station (data provided by Service d'Observation en Milieu Littoral, INSU-CNRS, Marseille). Rain: total rainfall in the 3 days prior to water sampling (Météo France data). Direction of wind: percentage of time during which wind is from the NW or SE during the 72 h period prior to sampling. Mean wind speed for each direction during the 72 h period prior to sampling (data from Service d'Observation/Centre d'Océanologie de Marseille – C. Yohia).

	Chl a ($\mu\text{g l}^{-1}$)	NH_4^+ ($\mu\text{mol l}^{-1}$)	NO_3^- ($\mu\text{mol l}^{-1}$)	Rain (mm)	Direction of wind		Mean wind speed (m s^{-1})	
					%NW	%SE	NW	SE
Spring	0.46	1.82	0.99	0.20	26	10	8.6	6.9
Summer	0.25	0.01	0.01	0.20	23	5	3.4	6.8
Autumn	0.13	0.03	0.15	0.00	41	10	16.5	4.7
Winter	0.46	0.07	0.02	3.20	64	10	16.2	8.2

On the contrary, SOM was marked by low variations for both isotopic and biochemical values in the Bay of Marseilles. To our knowledge, few data exist for seasonal variations of stable isotope signatures of coastal sediments, and the existing data concern environments which are too different to allow simple comparison. Seasonal variations are observed in deltaic sediments under the influence of the Danube (Banaru et al., 2007) and Rhône Rivers (Darnaude et al., 2004) or in a shallow eutrophic coastal Italian lagoon (Vizzini and Mazzola, 2003). In these environments, seasonal variations of SOM composition are linked with variations of riverine inputs and seasonal cycle of terrestrial primary producers. The artificial reefs located in the Bay of Marseilles are not under the influence of an important organic matter source able to drive seasonal variations, for the Huveaune River is small and its flow is diverted towards the Marseilles sewage system most of the time. As discussed above, sediment was mainly influenced by the exportation of detrital matter from *P. oceanica* seagrass meadow. Biomass and density of macro and meiofauna in sediment are mainly controlled by OM content (Fabiano et al., 1995). Inputs of labile compounds from macrophytes and epiphytes are a source of matter which is quickly used by consumers. To the contrary, the main production of *P. oceanica* is high molecular weight structure carbohydrates which are hard to use, which persist throughout the seasons and which are mainly responsible for the isotopic and biochemical values of SOM.

4.3. Influence of hydrodynamics

In the Bay of Marseilles, biochemical concentrations in POM were generally higher at V6 than at V3. $\delta^{13}\text{C}$ ratios were always lower at V6 than at V3, with marked differences in summer, autumn and winter. Mixing models based on isotopic ratios also showed different contributions of OM sources to V3 POM and to V6 POM. POM at each site appeared to be influenced by coastal POM, with marked inputs for V3 POM. Offshore POM was also an important contributor to V3 POM, whereas riverine matter carried by the Huveaune River influenced V6 POM. Even if phytoplanktonic production was generally predominant, these results demonstrated a different functioning of the waters masses. POM is not only a complex mixture of matter under the influence of different sources of OM, but it is also a transient pool which is strongly affected by hydrodynamic mechanisms. The studies performed on the dynamics of water masses in the Bay of Marseilles evidence their spatial heterogeneity and the influence of wind on their dynamics (Castelbon, 1972; Pradal and Millet, 2006). Wind measurements performed over 30 years show that the “mistral” (a wind blowing from the NW, 320–340° direction) is the main wind in the area (Pradal and Millet, 2006). In the Bay of Marseilles, the mistral creates two different currents. In the northern part of the Bay, an upwelling is created by this wind. It also causes the formation of a strong surface current which links the northern and southern parts of the Bay and which bathes V3. In the southern part of the sampling zone, two deep gyres are created by the mis-

tral. One is located near the coast close to the mouth of the Huveaune River and the other is further offshore and closer to V6 (Pradal and Millet, 2006). The mistral was blowing during most of the sampling period (Table 4) which may explain the spatial differences observed from summer to winter. The $\delta^{13}\text{C}$ values measured in V3 POM indicated inputs of phytoplanktonic OM, enhanced by upwelling and then driven to V3 by the strong surface current. The lowest $\delta^{13}\text{C}$ ratios measured in V6 POM highlighted the influence of riverine matter. During rain events, terrestrial matter is flushed out to sea by the Huveaune River and settles partially in the south of the Bay. This matter may then be re-suspended during mistral wind events and brought close to V6 by the combined action of the two gyres. The higher concentrations of lipids and proteins measured in V6 POM could also be linked with inputs of terrestrial proteins and lipids.

4.4. Influence of OM quality on trophic networks

Determination of the factors underlying the feeding choices of consumers has always been a complex question (Choat and Clements, 1998; Prado and Heck, 2011). In marine environments, various studies have demonstrated that the determination of biochemical concentration can give sufficient information to predict the distribution of organisms and consumption patterns (Fabiano et al., 1995; Rossi and Lardici, 2002; Grémare et al., 2003), particularly in coastal sediments where the quantity of nitrogen is considered to be a limiting factor (Tenore, 1988). In the Bay of Marseilles, a clear enrichment of POM as compared to SOM was observed, and was related to seasonal fluctuations of phytoplanktonic communities and to different influences of allochthonous organic matter sources, under the control of hydrodynamic and climatic parameters. In marine ecosystems, coupling between benthic and pelagic compartments is essential for their functioning (Danovaro et al., 2001; Frangoulis et al., 2011). Inputs of biochemically enriched OM falling through the water column represent an important source of matter for benthic communities (Covazzi Harriague et al., 2007; Quijón et al., 2008). A similar coupling may be important for the functioning of the artificial reefs deployed in the Bay of Marseilles. Inputs of enriched POM were likely to be one of the main sources of OM fueling the trophic networks based on filter feeders, which are abundant colonizers of the artificial reefs, as demonstrated in other artificial reef systems (Cheung et al., 2010). The combined use of both biochemical analyses to characterize the quality of OM and of isotopic analyses of all the organisms colonizing the artificial reefs would help to understand their trophic functioning and to bring new insights into trophic relationships and food selection factors of organisms in these new coastal ecosystems.

5. Conclusion

Our study was aimed to assess spatial and seasonal variation of isotopic and biochemical features of OM pools in the Bay of

Marseilles. Measured values showed differences in the functioning of these two pools. POM appeared to be a highly transient pool, mainly composed by phytoplankton with influences of riverine inputs on the southern part of the Bay. Variations were less marked in SOM and reflected the constant inputs of settling phytoplankton and *P. oceanica* detritus. Combined analyses were useful tools to characterize OM pools and were prerequisites to further understanding of the trophic networks newly established in the artificial reefs deployed in this zone. Future determination of isotopic ratios of consumers would bring insights into the differential integration of these two OM pools within the coastal trophic networks depending on their biochemical content and nutritional value.

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