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Sargassum beaching on mangrove sediments shifts microbial and crab metabolisms and enhances blue carbon storage

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Abstract

Benthic metabolism and net carbon accumulation in mangroves sediments strongly depend on the quantity and quality of organic matter (OM) supplied, including material brought by coastal waters such as the macroalgae *Sargassum* spp. Mesocosms were used to assess the effect of eutrophication by *Sargassum* on mangrove sediments. The concentration of fatty acids (FAs), organic carbon and its carbon isotopic signature, and the sediments–air CO_2 fluxes were used to follow the evolution of sedimentary OM in surface and subsurface sediments for 60 d. *Sargassum* beaching shifted microbial and crab metabolism, leading to a preferential degradation of the labile fraction of OM from both *Sargassum* ($\delta^{13}C = -17.7‰$ and high concentration of essential FAs) and mangrove leaves ($\delta^{13}C$: −28.9‰ and high concentrations of 18:2ω6 and 18:3ω3). Fatty acids composition of crabs hepatopancreas revealed they preferentially fed on *Sargassum* and these invertebrates also increased the particulate OM tidal export. In addition, microbial activity at the sediment surface was enhanced, as revealed by strong production of branched FAs and higher CO_2 fluxes in mesocosms containing *Sargassum*. However, *Sargassum* beaching also increased the transfer and preservation of more refractory OM from mangrove leaves found in higher quantity in subsurface sediments (6–8 cm) after 60 d. Inputs of macroalgae induced a negative priming effect and enhanced the preservation of blue carbon in the sediments. This negative priming effect was enhanced by crab activities. These biotic interactions that include microbial communities apparently make mangrove efficient in storing carbon in a context of growing eutrophication of the tropical ocean.

Among blue carbon ecosystems, the rate of carbon storage in sediments of mangrove forests is estimated at 41 Tg C yr^{-1} (Wang et al. 2021). Before reaching the long-lasting carbon strata, organic matter (OM) present in the mangrove litter will first need to cross a layer of intense diagenesis in the top sediments 10 cm (Lallier-Vergès et al. 2008; Crémière et al. 2017). This transfer is strongly impacted by emersion cycles, flooding, porewater tidal pumping, and the occurrence of successive oxic and anoxic conditions, which potentially enhance diagenesis (Sun et al. 2002). Organic matter quality and transfer is also drastically modified by microbial degradation and intense activity of bioturbators (Kristensen et al. 2008; Alongi 2014).

Human settlements on coastlines generate a eutrophication of marine ecosystems, which become enriched in nutrients and OM from direct urban inputs, enhanced productivity of phytoplankton and pelagic macroalgae, and aquaculture (Nixon 1995; van Beusekom 2018). Eutrophication leads not only to an additional supply of OM in mangroves, but also potentially increases the sedimentary OM (SOM) lability, as most of these additional OM sources are composed of much more biodegradable molecules (e.g., fatty acids [FAs], sugars, …) than those (e.g., lignin) predominating in mangrove material (Kristensen et al. 2008; Chynel et al. 2022). Higher quantity and

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lability of SOM increase benthic remineralization rates in eutrophic mangroves (Barroso et al. 2022).

In terrestrial soils, Fontaine et al. (2003) showed that an input of fresh OM accelerates the growth of specialized degrading microorganisms which destabilizes carbon stocks leading to a phenomenon called "priming effect." In mangroves, once deposited on the sediment, the litter is colonized by microbes which makes this OM much easily ingested and assimilated by benthic organisms such as crabs, the most abundant macrofauna taxa in mangroves sediments (Kristensen et al. 2008; Nordhaus et al. 2011). Among them, fiddler crabs mainly feed on litter detritus, bacteria, and microphytobenthos (Meziane et al. 2002) and therefore decrease the carbon concentration in the top millimeters of the sediments (Kristensen and Alongi 2006). Eutrophication of mangrove sediments has several impacts on fiddler crab communities such as their abundance, their feeding activity (Penha-Lopes et al. 2009) and their metabolism (Costa and Soares-Gomes 2015). Nonetheless, during eutrophication, these crabs may enhance respiration-induced CO_2 fluxes from sediments (Nielsen et al. 2003; Barroso et al. 2022).

To characterize the dynamics of OM in mangrove sediments, various biogeochemical proxies are used. Among them, FAs and $\delta^{13}C$ signature of bulk sediments are useful to identify sources and lability of OM (Dunn et al. 2008). Similarly, these tracers highlight processes generated by eutrophication, such as an enhanced microbial loop (Chynel et al. 2022). In addition, the measurement of CO_2 fluxes to the atmosphere allows to detect changes in benthic metabolism due to the eutrophication (Barroso et al. 2022).

The Guadeloupe island (French West Indies) hosts about 3200 ha of mangroves (Taureau et al. 2019) with larges stocks of well-preserved carbon in their sediments (Lallier-Vergès et al. 2008). In the last decades, the island has been impacted by massive beaching of the pelagic macroalgae *Sargassum* (*Sargassum fluitans* and *Sargassum natans*; Ody et al. 2019). *Sargassum* are a potential carbon sink when located in the water column or on the ocean floor (Gouvêa et al. 2020). However, their potential effect on mangroves blue carbon reservoir is still unknown.

In the present study, we used experimental tanks containing intact 20 cm of mangrove sediment, and we simulated tidal inundation to assess OM transfers and degradation in the presence and absence of crabs. Known quantities of *Avicennia germinans* leaves and *Sargassum* thalles were added daily to simulate natural and eutrophication conditions. We measured FAs concentrations, $\delta^{13}C$ isotopic signature of organic carbon (OC) and sediment-air CO_2 fluxes to describe the effects of *Sargassum* spp. thalles and fiddler crab's activity on the remineralization intensity and the transfer of OM in mangrove sediments.

Materials and methods

Experimental design

Twenty-four intact blocks of sediments were collected in the inland zone of the mangrove area of Souffleur (Port-Louis, Guadeloupe) in August 2020. Sediment blocks were placed in tanks (width 20 cm, length 25 cm, height 20 cm; Supporting Information Fig. S1) and kept in the laboratory for 1 week before starting the experiment. Male fiddler crabs of the genus *Minuca* spp. (Ocypodidae) were collected from the same mangrove and then placed in stabulation in empty containers for a week in order to empty their stomach. At the same location, mangrove leaves, surface sediments (1 cm of sediments), and 8-cm sediment cores were sampled ($n = 4$). Each of the four cores was sliced into four depths: 0–2, 2–4, 4–6, and 6–8 cm. Fresh floating *Sargassum* thalles were sampled in the bay of Anse à l'Eau.

The 24 tanks (surface 0.05 m^2) were separated in 3 treatments (8 tanks by treatment): control (no OM inputs), leaves (L: daily addition of approx. 1.3 g wet weight of mangrove leaves), and leaves + *Sargassum* (L + S: daily addition of 1.3 g wet weight of mangrove leaves and 7.5 g wet weight of *Sargassum*). These quantities were chosen to simulate typical rates of litter fall in such mangrove (Twilley et al. 1986) and rates of *Sargassum* deposition within the range of those occurring in Guadeloupe during the beaching season (Bernard et al. 2022). Dry weight (dw) of the daily inputs (0.5 g of mangrove leaves in both L and L + S tanks and 1.6 g of *Sargassum* in L + S tanks) was calculated after drying material at 60°C for 24 h. Average water contents were 79% and 63% in *Sargassum* thalles and mangrove leaves, respectively. Daily OC supply was 2.8 gC m^{-2} d^{-1} in L tanks and 11.4 gC m^{-2} d^{-1} in L + S tanks. Four replicates of each treatment contained one crab and the four other replicates did not contain crab. Replicate tanks were randomly dispatched in the lab. Each day, about 60 liters of seawater were sampled and filtered through GF/F filters (0.7 μm) prior to being added to the tanks to avoid contamination of sediments by marine particulate OM (POM). For logistic reasons, tidal inundation was simulated diurnally instead of semi-diurnally, by gently filling each tank with 2.5 liters of filtered sea water every day at 5 p.m. and then evacuated at 7 a.m. through a tap located 18 cm below the surface of the sediment (Supporting Information Fig. S1). We assume that positioning the tap at that depth allows to evacuate surface porewater in a way representative of in situ conditions in the Caribbean Sea, with a tidal amplitude between 15 and 25 cm.

Sampling

The experiment lasted 60 d. At each sampling time (T0, T8, T15, T30, T45, and T60), the sea water was drained from each tank using the tap installed for that purpose and filtered through GF/F filters (0.7 μm) to analyze POM. During the simulated low tide, static gas chambers (10 × 10 × 10 cm) were placed on the sediments and first left open for 10 min to avoid the disturbance of CO_2 concentrations due to the positioning of the chamber. Then, the air inside the chamber was purged and replaced by ambient air with an air pump at the beginning of each flux measurement. The initial gas sample was taken, then the chamber was left closed for 2 h on the sediment, and a gas sample was taken every hour with a syringe though a rubber septum. Before each gas sampling, the gas in

the chamber was homogenized with the syringe to destroy an eventual stratification. Gas samples were transferred to pre-evacuated exetainer tubes and stored at ambient temperature and in the dark until CO_2 analysis in the laboratory. Just after chambers measurements, five replicates of surface sediments were randomly sampled with a spatula in each tank at each sampling time and then pooled. Intact litter was temporarily lifted to collect the sediment below. The same sediment area was never sampled twice during the whole experiment.

On the last day of the experiment (T60), living crabs as well as three 8-cm-long sediment cores were collected in each tank. Crabs were dissected, and hepatopancreas were isolated. Each core was subdivided into four segments of 2 cm. The three segments at the same depth coming from the replicates of the same tank were pooled. Immediately after collection, filters containing POM, sediments, and hepatopancreas samples were stored at −20°C. At the end of the experiment, all samples were freeze dried and stored again at −20°C.

Fatty acids analysis

Fatty acids were analyzed for surface and 6–8 cm deep sediments, filters (T0, T8, T15, T30, T60), mangrove leaves, and *Sargassum* according to Meziane et al. (2007). Fatty acids methyl esters in chloroform are quantified by gas chromatography (GC; Agilent 8890) coupled to a flame ionizer and then identified by comparing chromatograms with those generated by a GC coupled to a mass spectrometer (Agilent 5977B) and with a commercial standard (Supelco® 37) and laboratory's library. Fatty acid concentrations were calculated using the added 23 : 0 (internal standard) known concentration, assuming that they all undergo equivalent losses. The concentration of FAs is given by the following equation:

$$C_{FA} = \frac{A_{FA}}{A_i} \times \frac{C_i}{W_s} \times 1\,\mu L$$

where C_{FA} is FA concentration ($\mu g\ g^{-1}$), A_{FA} the peak area of FAs, A_i is the peak area of the internal standard, C_i is the concentration of the internal standard ($\mu g\ \mu L^{-1}$), and W_S is sample weight (g).

Isotopic analysis

The $\delta^{13}C$ signatures were analyzed for surface and 6–8 cm deep sediments, filters (T0, T15, T30, T60), mangrove leaves, and *Sargassum*. Before analyses, carbonates were removed from sediments and filters by acidification. Sediments were immersed in 5% HCl for 24 h, and filters were fumigated with 37% HCl for 6 h. Sediments and filters were analyzed at the LIENS laboratory (La Rochelle, France) where they were processed by a continuous flow isotope mass spectrometer (DeltaV Advantage, Thermo Finnigan) coupled to an elemental analyzer (Flash EA 1112 Series, Thermo Finnigan). Plant tissues were analyzed for $\delta^{13}C$ signatures at the Center for Physical Science and Technology (Vilnius, Lithuania), using an Elemental Analyzer (Flash EA 1112 Series, Thermo Finnigan) coupled to an Isotope Ratio Mass Spectrometer (DeltaV Advantage, Thermo Finnigan). Stable isotope results are reported in parts per thousand (‰), using the standard delta notation ($\delta^{13}C$) relative to international standards: VPDB.

Gas analysis

Concentration of CO_2 in gas samples was analyzed by gas chromatography coupled with a methanizer and a flame ionization detector (SRI 8610C GC-FID) at laboratory of Géosciences Environnement Toulouse (GET, Toulouse, France). Calibration was carried out with certified CO_2/N_2 gas mixtures of 400, 1000, and 3000 ppm (Air Liquide® France).

Data processing

We used an isotopic mixing model based on mass conservation of total OC, ^{12}C, and ^{13}C during the mixing of mangrove sediments with leaves and/or *Sargassum* in the different treatments. The calculations consider as the initial sedimentary OC and $\delta^{13}C$ values observed in situ, which were not significantly different from those obtained in the control tanks at T60 without leaves and *Sargassum* addition. The theoretical changes in OC and $\delta^{13}C$ in the different tanks were calculated by iterations, increasing the mass of added leaves and *Sargassum* according to the conservation of OC:

$$\%OC_{mix} = \frac{\%OC_{Sed} W_{Sed} + \%OC_L W_L + \%OC_S W_S}{W_{Sed} + W_L + W_S}$$

where $\%OC_{mix}$, $\%OC_{Sed}$, $\%OC_L$, $\%OC_S$ and W_{mix}, W_{Sed}, W_L, W_S are the OC content (%OC in percent) and the weight (W in grams) of the mixture, the initial sediment, the leaves, and the *Sargassum*, respectively, and the conservation of stable isotopes:

$$\delta^{13}C_{mix} = \frac{\delta^{13}C_{Sed}\%OC_{Sed} W_{Sed} + \delta^{13}C_L \%OC_L W_L + \delta^{13}C_S \%OC_S W_S}{\%OC_{Sed} W_{Sed} + \%OC_L W_L + \%OC_{Sed} W_S}$$

where $\delta^{13}C_{mix}$, $\delta^{13}C_{Sed}$, $\delta^{13}C_L$, and $\delta^{13}C_S$ are the carbon stable isotope signatures (in ‰) of the sediment mixture in the tank during the incubations, of the initial sediment, of the leaves, and of the *Sargassum*, respectively. From the observed values of $\%OC_{mix}$ and $\delta^{13}C_{mix}$ at T60 in the different treatments at different depths, in the leaves and *Sargassum* material, and in the initial sediment and control incubation, we could calculate the respective contribution of leave material W_L and of *Sargassum* material W_S to the increase (enrichment) in OC in the different mesocosms.

Statistical analysis

Due to the nonhomogeneous nature of the variance nonparametric tests were performed: Wilcoxon test for comparison of FAs, OC, and $\delta^{13}C$ means in sediments (surface and subsurface) and POM between treatments as well as spearman

rank test for correlation between FAs concentrations in surface sediments and time (significance level $p < 0.05$). Differences in FAs concentration in surface and subsurface sediments among treatments were tested using permutational multivariate ANOVA with a three-factor design (5000 residual permutations under a reduced model), with treatment (control, L, and L + S), crab presence and time (or sediments depth). We also performed permutational multivariate ANOVA (5000 residual permutations under a reduced model) analysis with a Bonferroni correction by grouping the data according to treatment and analyzing effect of crabs and time on FAs concentrations (significance level $p < 0.05$). Data were analyzed with R software (version 4.0.5).

Results

Fatty acids composition in mangrove leaves and *Sargassum* thalles

Concentrations of FAs and OC of *Avicennia germinans* leaves and *Sargassum* spp. thalles are presented in Table 1. Although the concentrations of OC and total fatty acids (TFAs) were similar ($p > 0.05$) in mangrove leaves and *Sargassum* thalles, these two sources of OM had very different isotopic signatures and FA composition. The concentrations of 18:2ω6 and 18:3ω3 were, respectively, 10 and 6 times higher in mangrove leaves than in *Sargassum* thalles ($p < 0.001$). Long-chain FAs (LCFAs: 24:0 + 26:0 + 28:0 + 30:0) were present in mangrove leaves but absent in *Sargassum* thalles. Among the polyunsaturated FAs (PUFAs), 20:4ω6, 20:5ω3, and 22:6ω3 (here called essential FAs [EFAs]) were detected in *Sargassum* thalles but not in mangrove leaves. Bacterial markers are detected in both plants (branched FAs [BrFAs] Iso and Anteiso 13:0 + 15:0 + 17:0 + 19:0).

Table 1. Concentration of fatty acids (average ± standard deviation; $\mu g\ g^{-1}$ dw) in mangrove leaves and *Sargassum* thalles.

	Mangrove leaves	*Sargassum* thalles
16:0	1195.7 ± 325.3	647.3 ± 200.0
16:1ω7	17.7 ± 9.5	114 ± 33.8
18:0	198.2 ± 77.9	95.9 ± 34.5
18:1ω7	54.3 ± 27.2	64 ± 12.8
18:1ω9	1027.5 ± 445.5	165.1 ± 40.4
18:2ω6	493.5 ± 275.2	49.5 ± 39.2
18:3ω3	1630.1 ± 811.4	37.4 ± 10.7
20:4ω6	BDL	169.5 ± 54.0
20:5ω3	BDL	54.2 ± 27.0
22:6ω3	BDL	44.1 ± 23.9
TFAs	5244.4 ± 1932.8	1824.4 ± 589.9
LCFAs	107.2 ± 48.7	BDL
BrFAs	34.4 ± 39.6	28.6 ± 7.6

BDL, below detection limit; BrFAs, branched fatty acids; dw, dry weight; LCFAs, long-chain fatty acids; TFAs, total fatty acids.

Litter fragmentation by crabs

In the absence of crabs, litter in L and in L + S tanks, remained abundant and accumulated at surface sediments during the whole experimental period (Fig. 1e,f). In the presence of crabs, both leaves and macroalgal material continuously disappeared (Fig. 1b,c), emphasizing the fundamental role of these invertebrates in the transfer and recycling of OM.

Fatty acids concentrations in crab hepatopancreas

The concentration of TFAs was significantly higher in hepatopancreas of crabs in the L + S tanks compared to crabs in the other tanks ($p < 0.001$; Table 2). In the hepatopancreas of crabs, the concentration of Σ18PUFAs was higher in L tanks compared to control tanks ($p < 0.05$). Conversely its concentration was similar in the hepatopancreas of crabs in L and L + S tanks ($p > 0.05$; Table 2). All other FA groups have higher concentrations in hepatopancreas of crabs in L + S tanks compared to other tanks ($p < 0.01$).

CO_2 fluxes

In control tanks the fluxes of CO_2 to the atmosphere were constant over time and show no difference whether the crabs were present or not ($p > 0.05$; Fig. 2a). In L tanks, the CO_2 fluxes increased with incubation time ($p < 0.001$; Fig. 2b) and were similar in the presence or absence of crabs ($p > 0.05$). In the L + S treatments, the CO_2 emission was positively correlated with time ($p < 0.001$). In L + S tanks, CO_2 fluxes increased between T0 and T15 and then decreased but the values remained 5–8 times higher than in the other treatments. In the L + S treatment CO_2 fluxes were significantly lower in the presence of crabs ($p < 0.05$; Fig. 2d).

Export of POM

After 60 d of experiment, in Control, L, and L + S tanks, the total carbon export via POM by the simulated tidal cycle was, respectively, 2.8, 2.6, and 3.6 times higher in the presence of crabs compared to no crab conditions ($p < 0.05$; Fig. 3). This export was higher in L + S tanks with and without crabs than in all other tanks ($p < 0.05$).

The $\delta^{13}C$ isotopic signature of POM was stable over time in all control tanks ($p > 0.05$) and decreased significantly over time in all L tanks ($p < 0.001$; Fig. 3). The $\delta^{13}C$ isotopic signature of POM was enriched in L + S tanks in the absence of crabs compared to with crabs at all times ($p < 0.05$) except at T0 ($p > 0.05$; Fig. 3). $\delta^{13}C$ signatures of POM were significantly enriched at all times in all L + S tanks compared to all other tanks ($p < 0.05$).

Temporal changes of FA concentrations in surface sediments and in subsurface sediment (6–8 cm layer) at T60

Independently of the presence or absence of crabs, FA concentrations were significantly influenced by time in control (permutational multivariate ANOVA; $p < 0.01$) and in L tanks

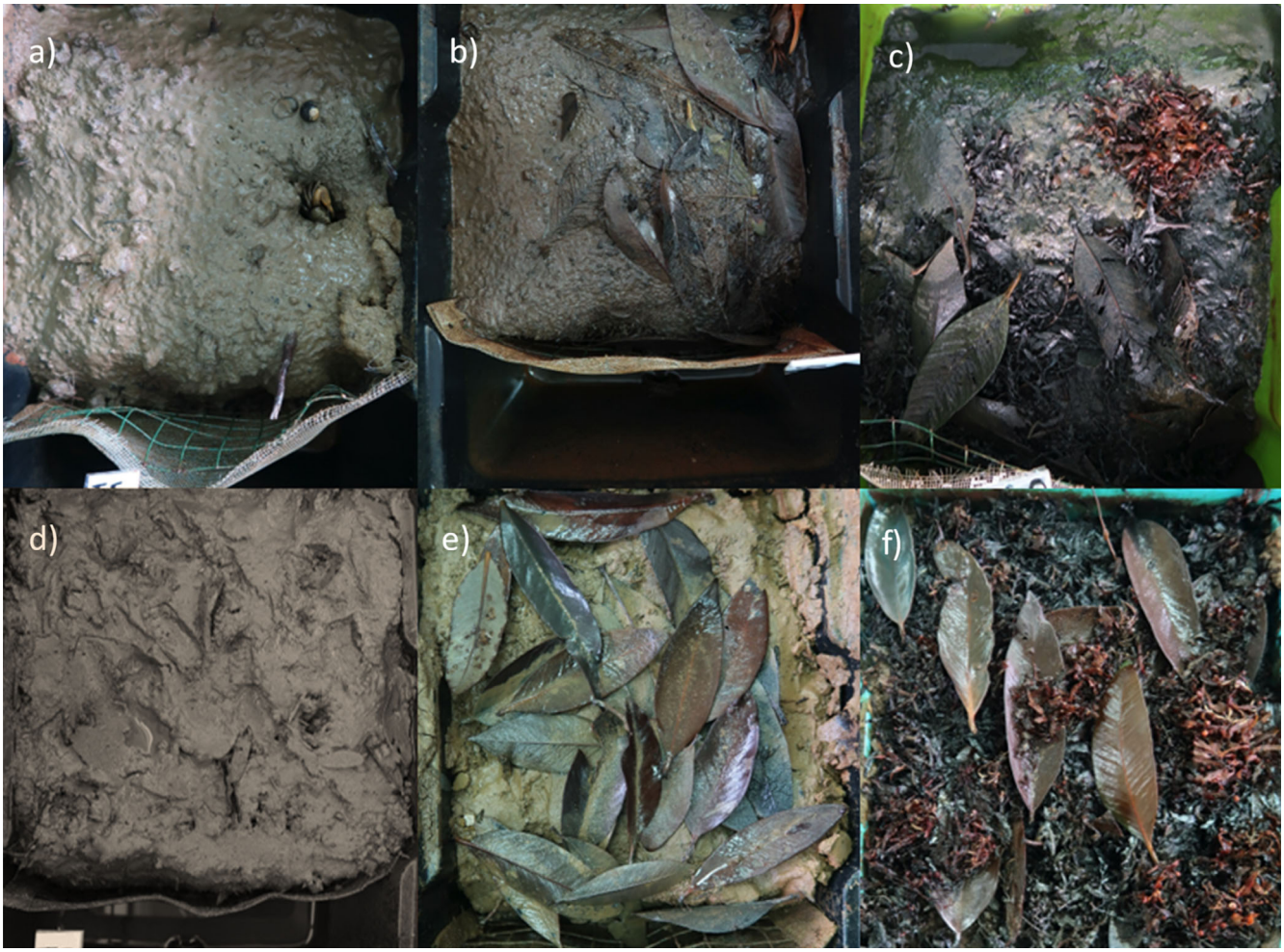

Fig. 1. Photos of representative tanks at T60. Top: with crabs; bottom: without crabs. (**a**, **d**) Control; (**b**, **e**) daily addition of one leaf (L); (**c**, **f**) daily addition of one leaf and *Sargassum* thalles (L + S); (**a**–**c**) with crabs; (**d**–**f**) without crabs.

Table 2. Fatty acids concentration (average ± standard deviation; μg g^{-1} dw) in hepatopancreas of *Minuca* spp. collected at T60) in the three experimental treatments (control, L, and L + S).

	Control	L	L + S
TFAs	27.8 ± 6.0	44.2 ± 21.4	157.2 ± 47.1
Σ18PUFAs	2.0 ± 0.6	6.0 ± 3.8	8.8 ± 2.8
EFAs	10.2 ± 2.0	10.0 ± 2.8	31.9 ± 17.9
PUFAs	12.8 ± 2.7	16.7 ± 6.2	43.7 ± 20.5
BrFAs	0.7 ± 0.3	0.9 ± 0.5	7.5 ± 5.7

BrFAs, branched fatty acids; w, dry weight; EFAs, essential fatty acids; L, leaves; L + S, leaves + *Sargassum*; PUFAs, polyunsaturated fatty acids; TFAs, total fatty acids.

($p < 0.001$). This effect was evidenced by the significant decrease over time of the concentration of all FAs (except EFAs and BrFAs $p > 0.05$; Fig. 4) in the surface sediment of these two treatments (*rho* ranged between −0.67 and −0.45; $p < 0.01$; Fig. 4).

In the presence of crabs, the concentration of all FA groups except LCFAs increased over time ($p < 0.01$), which led to higher concentrations of all FA groups than in the L + S tanks without crabs ($p < 0.05$) and in all others control and L tanks ($p < 0.001$). At T60, the concentrations of all FA groups, except LCFAs, was higher in the L + S tanks, with or without crabs, than in the control and L tanks ($p < 0.05$).

Stable isotopes mixing model

The fate of OM originating from *Sargassum* thalles could be clearly differentiated from that coming from mangrove leaves thanks to their isotopic signature (respectively, −17.7‰ ± 0.8‰ and −28.9‰ ± 0.5‰; Table 3). After the stabulation period, during the experiment from T0 to T60, OC concentration at surface sediment significantly increased in L + S tanks with and without crabs, and in L tanks with crabs ($p < 0.05$; Table 3). At T60, in L tanks, $\delta^{13}C$ of the surface sediment was depleted ($p < 0.05$) while that of L + S tanks was enriched ($p < 0.05$; Table 3). In subsurface (6–8 cm) sediments at T60,

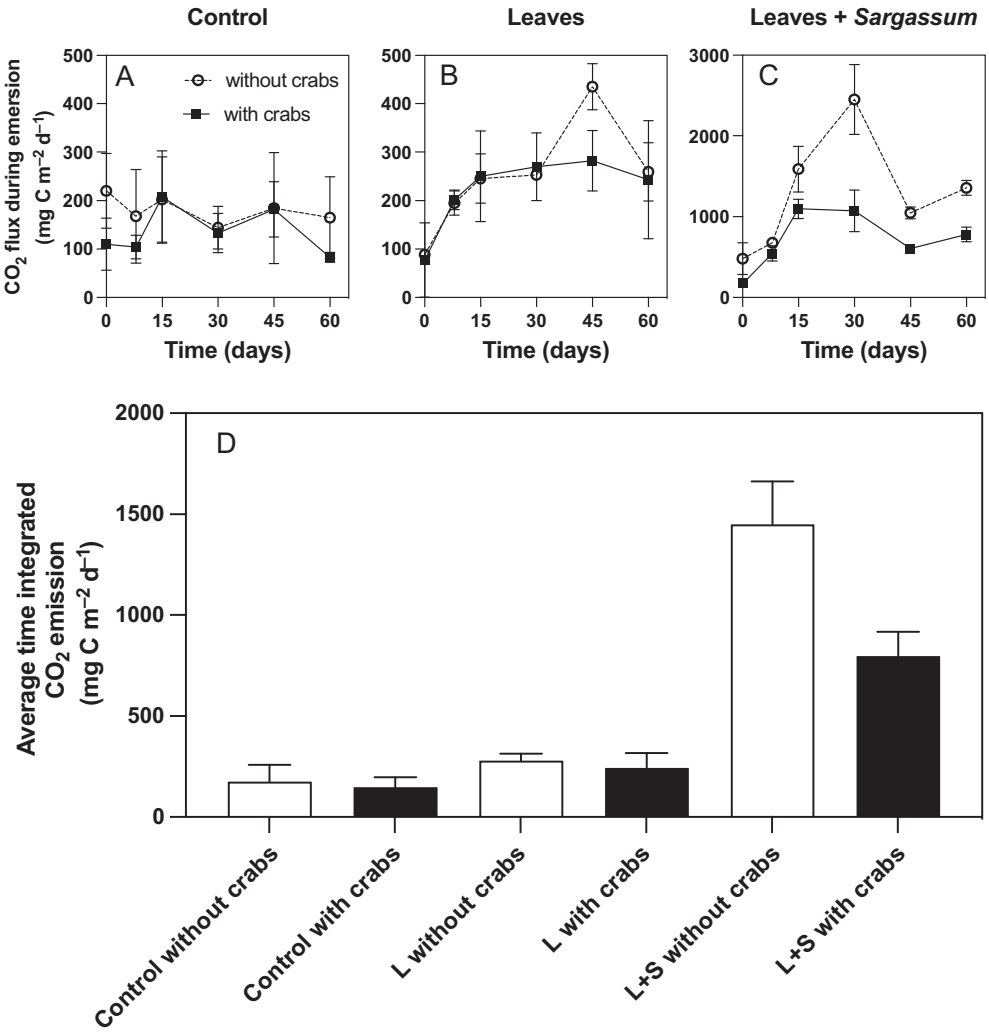

Fig. 2. Sediment–air CO_2 fluxes during the emersion (mg C $m^{-2}d^{-1}$, during 12 h of emersion). (**a**–**b**) The time courses of CO_2 fluxes in the different treatments during the 60 d of experiment (note the different scale for the L + S treatment). (**d**) Average time-integrated CO_2 fluxes.

only the L + S tanks (with and without crabs) had higher OC concentration compared to all other tanks ($p < 0.01$; Table 3). When comparing surface and subsurface sediments at T60, a distinct pattern was identified in terms of $\delta^{13}C$ isotopic signature in the L + S tanks both in the presence and absence of crabs. Indeed, enriched $\delta^{13}C$ from *Sargassum* was present at the surface but not at 6–8 cm (Supporting Information Fig. S2). According to the isotopic mixing model, *Sargassum* contribution to the OC enrichment at this depth was at maximum 4% in the L + S tank with crabs (Table 3) showing that remineralization of *Sargassum* OM was extremely efficient and that this material was not preserved in the subsurface. In contrast, the $\delta^{13}C$ signature of the sediments at 6–8 cm was depleted in L + S tanks (with and without crabs) compared to all other tanks ($p < 0.05$; Table 3). The observed OC enrichment at 6–8 cm in L + S tanks compared control tanks (12.3 ± 2.4 mg C g^{-1} without crabs and 21.3 ± 2.6 mg C g^{-1}), was caused in majority (96–100%) by an incorporation of ^{13}C-depleted OC from leaves (Table 3).

Discussion

Representativity of mesocosms conditions for the sedimentary carbon balance

Our experimental mesocosms were designed to provide a quantitative analysis of C transfers in the top must bio-reactive 10 cm of the sediment, when *Sargassum* thalles settle in a mangrove ecosystem. Sediment used in the mesocosms was collected in a natural mangrove area, which has an OC concentration and $\delta^{13}C$ signature of its surface (on average 31.7 mg g^{-1} and 28.2‰) that were in the range of those measured in other mangroves around the world (Kennedy et al. 2004; Adame and Fry 2016).

Representativity of the mesocosm experiment must be first analyzed in the light of the evolution of OC concentrations at

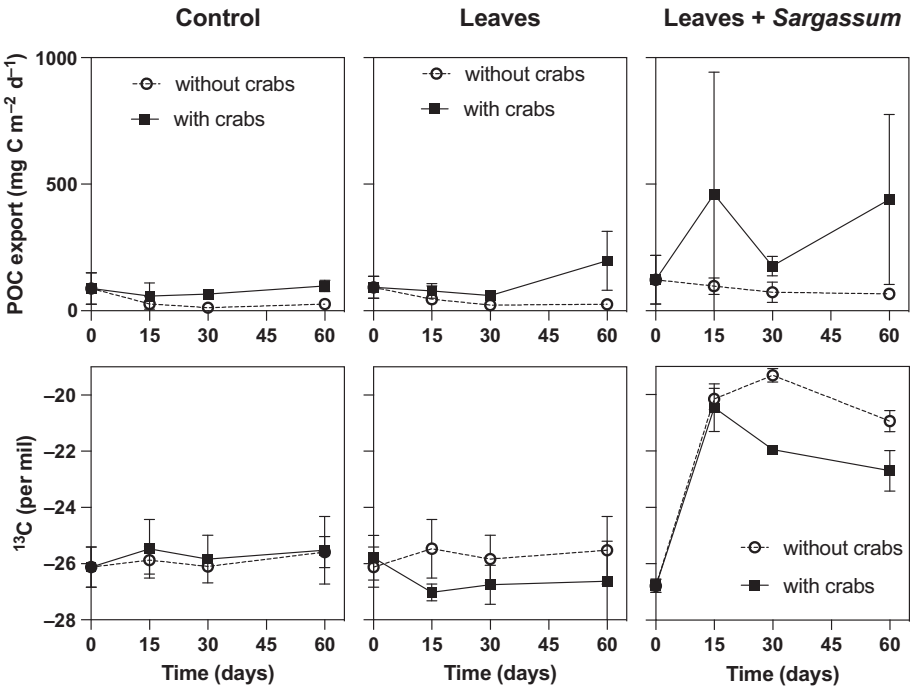

Fig. 3. Top: evolution of particulate OC export by the simulated tide (mg C $m^{-2}d^{-1}$) and bottom: temporal dynamic of $\delta^{13}C$ signature of POM in the three experimental treatments (control, L, and L + S). Error bars are standard deviations from the mean of three tanks (treatment + absence/presence of crabs) and six tanks at T0, before the contribution of crabs. L, leaves; L + S, leaves + *Sargassum*; OC, organic carbon; POM, particulate organic matter.

different depths and treatments. There was a strong depletion in OC from the field conditions to the T0 conditions (Table 3), due to an apparent enhancement of oxidation of OM during sampling, transport, and stabulation, promoted by partial reoxygenation, as previously reported in bare sediments (Lovelock et al. 2011). The small loss of the refractory part of FAs (LCFAs) compared to other FAs indicates that the labile part of the SOM was preferentially degraded during the stabulation period (Supporting Information Table S1), coherent with finding by Lallier-Vergès et al. (2008). This fast initial OM mineralization decreased OC by 67% and TFAs by 29% (Table 3; Supporting Information Table S1). Then, during the experiment from T0 to T60, there was a partial replenishment in OC and FAs in all tanks with OM litter additions, leaves, and/or *Sargassum*, to reach at T60 values closed to in situ conditions (37.5 ± 6.7 mg C g^{-1}) in the L + S tank with crabs at the surface (36.5 ± 2.2 mg C g^{-1}) and at 6–8 cm depth (30.3 ± 2.4 mg C g^{-1}). Organic carbon contents were also consistently 17–27% higher in surface than in subsurface sediment, but strongly dependent on the addition of mangrove leaves and *Sargassum* thalles and the presence or absence of crabs. This indicates that, although the experiment occurred during a replenishment transient period after the stabulation period, the comparison of control with other treatments at T60 provides quantitative information on mechanisms controlling the fate of the added fresh OM, and the balance between degradation, export, and incorporation in the sediment. This includes also litter fractionation and bioturbation by crabs and lateral and downward transport due to a microtidal flooding and drainage.

When analyzing quantitatively the fate of the added C in L and L + S tanks, our experimental design was not sufficient to document all C fluxes and close a full carbon budget. However, the quantitative comparison of the inputs, with the quantified outputs and storage for 60 d was possible for the L and L + S tanks (Supporting Information Table S2). Depending on the treatments, when compared to the litter addition in the L tanks (2.8 mg C m^{-2} d^{-1}) and the L + S tanks (11.4 mg C m^{-2} d^{-1}) POC tidal export accounted for 0.8–3.7%, CO_2 emission during emersion for 7–13%, and OC accumulation for 7–31% in the 0–2 cm surface layer and 9–18% in the 6–8 cm layer. Unaccounted carbon in the budget varied between 38% and 71%, apparently sufficient to account for the OC accumulation in the other sediment layers (2–6 cm and below 8 cm), for the tidal pumping of dissolved OC and inorganic C, and for the water–air CO_2 exchange during immersion periods. Another indication that the mesocosms satisfactorily mimics in situ conditions comes from the proportions between the POC export and CO_2 fluxes, coherent with those in global C fluxes estimates in mangroves (Alongi 2022; Adame et al. 2024).

Sargassum degradation and crab activity promote the incorporation of litter OM to surface sediments

The slow degradation in surface sediment of the labile OM (EFAs and Σ18PUFAs) as well as the refractory compounds

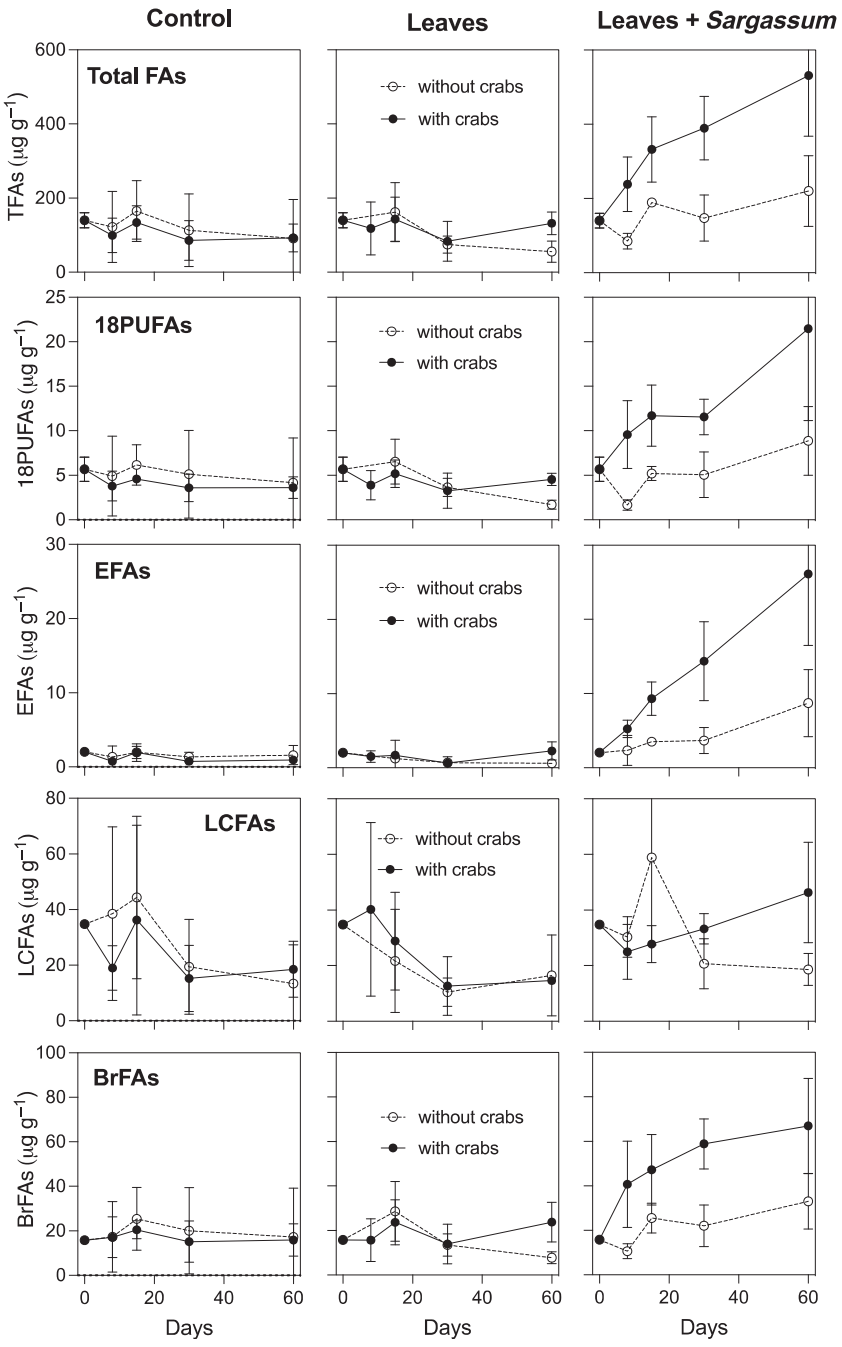

Fig. 4. Temporal change of FAs concentrations (μg g^{-1} dw) in surface sediments in the three experimental treatments (control, L, and L + S), with and without crabs. Σ18PUFAs, 18:2ω6 + 18:3ω3; BrFAs, branched fatty acids; dw, dry weight; EFAs, essential fatty acids; FAs, fatty acids; L, leaves; L + S, leaves + *Sargassum*; LCFAs: long-chain fatty acids; PUFAs, polyunsaturated fatty acids; TFAs, total fatty acids.

(LCFAs) in the control tanks during the experiment (Fig. 4) was reflected in the small amount of microbial metabolism as revealed by the low CO_2 fluxes during emersion (Fig. 2a). Thus, without addition of fresh OM, the rate of degradation of SOM was mainly controlled by the availability of labile compounds as previously observed in natural mangrove sediments (Marchand et al. 2005). In the surface of these control tanks, crabs had no influence on the quantity and quality of SOM as reflected by OC concentration, δ^{13}C signature and FA composition (Figs. 1, 4; Table 3).

When fresh leaves (L) and/or *Sargassum* (L + S) were added to the tanks, degradation and export of SOM with different labilities occurred at different paces. In surface sediments of L tanks without crabs, δ^{13}C signature and FAs composition

Table 3. Organic carbon contents and carbon isotopic compositions in experimental tanks and results of the isotopic mixing model (OC enrichment in 60 d).

			OC enrichments in 60 d		
mg C g^{-1}	OC, mg g^{-1}	$\delta^{13}C$, ‰	Total OC, mg g^{-1}	OC from leaves, mg g^{-1} (%)	OC from *Sargassum*, mg g^{-1} (%)
Litters					
Leaves	297.4 ± 16.0	−28.9 ± 0.5			
Sargassum	273.4 ± 14.0	−17.7 ± 0.8			
Surface sediment					
In situ	37.5 ± 6.7	−28.3 ± 0.2			
T0	12.1 ± 1.7	−24.8 ± 0.3			
T60 control without crabs	13.7 ± 1.1	−25.2 ± 0.2	—	—	—
T60 control with crabs	13.4 ± 0.8	−24.7 ± 0.2	—	—	—
T60 L without crabs	15.0 ± 0.9	−25.5 ± 0.2	1.9 ± 1.5	1.9 ± 1.5 (100%)	0 (0%)
T60 L with crabs	18.8 ± 2.6	−26.8 ± 0.7	5.7 ± 2.9	5.7 ± 2.9 (100%)	0 (0%)
T60 L + S without crabs	28.1 ± 3.1	−25.2 ± 0.3	15.1 ± 3.4	10.4 ± 2.3 (69%)	4.6 ± 1.0 (31%)
T60 L + S with crabs	36.5 ± 2.2	−22.4 ± 0.8	23.4 ± 2.5	7.5 ± 0.8 (32%)	15.9 ± 1.7 (68%)
6–8 cm sediment					
In situ	26.0 ± 2.4	−28.0 ± 0.1			
T60 control without crabs	8.7 ± 1.2	−24.9 ± 0.2	—	—	—
T60 control with crabs	9.4 ± 0.4	−25.2 ± 0.2	—	—	—
T60 L without crabs	11.5 ± 2.5	−25.9 ± 0.6	2.4 ± 2.6	2.4 ± 2.6 (100%)	0 (0%)
T60 L with crabs	13.7 ± 1.9	−25.4 ± 0.3	4.7 ± 2.0	4.7 ± 2.0 (100%)	0 (0%)
T60 L without crabs	21.4 ± 2.3	−27.6 ± 0.4	12.3 ± 2.4	12.3 ± 2.4 (100%)	0 (0%)
T60 L + S with crabs	30.3 ± 2.4	−27.5 ± 1.1	21.3 ± 2.6	20.4 ± 2.5 (96%)	0.8 ± 0.1 (4%)

remained similar to those in control tanks indicating that fresh OM from leaves was not efficiently incorporated (Table 3; Fig. 4).

The experiment highlights the role of crabs in the fate of the deposited OM. Indeed, in the absence of crabs, deposited mangrove leaves and *Sargassum* thalles form a litter at the sediment surface (Fig. 1). For instance, it has been reported that crabs can remove up to 90% of total litterfall in mangrove forests (Friesen et al. 2018). In the presence of crabs, $\delta^{13}C$ signature of surface sediments became more depleted in L tanks (Table 3) showing that the activity of these invertebrates plays a role in the incorporation of leaf litter OM and significantly increase the tidal export of POC (Fig. 3). However, with only leaves as food resource, these fiddler crabs remained starved as revealed by the similar concentrations of TFAs in their hepatopancreas, crucial to the metabolism of crustaceans (Sánchez-Paz et al. 2006), in control and L tanks (Table 2).

CO_2 fluxes in L tanks were modest compared to the quantity of added OC (< 5% mineralized in 60 d; Fig. 2) showing that remineralization of added leaves OM was slow either in the presence or absence of crabs. Nevertheless, these CO_2 fluxes were in the range of those measured in mangroves around the world (Hien et al. 2018; Barroso et al. 2022). Yet, the respiration slightly increased over time due to the continuous addition of leaf litter during the experiment. Such a positive correlation between sediment-air CO_2 fluxes and the quantity of litterfall was previously reported in natural mangroves by Lovelock (2008).

The addition of *Sargassum* in L + S tanks lead to the increase of the OC and FAs concentration in surface sediments (Table 3; Fig. 4). Thus, this simulated eutrophication enhanced the incorporation of OM from the leaves *Sargassum* litter complex to surface sediment, inducing an enrichment of the $\delta^{13}C$ signature of SOM after 60 experimental days (Table 3). Organic matter incorporation was further enhanced in the presence of crabs. Isotopic mixing model indicate that at T60, incubation in the L + S tanks without crabs, leaves material contributed proportionally much more than *Sargassum* thalles to the surface sediment OC enrichment (69% of the total SOM Table 3) than expected from the proportions of the two sources added into the tanks (25% of leaves and 75% of *Sargassum* thalles). The lower relative contribution of *Sargassum* suggests a preferential use of this macroalgae by benthic microbes, consistent with the amount of emitted CO_2 and the increase of BrFAs in surface sediment (Figs. 3, 4). The CO_2 emissions in L + S tanks were in the range of those measured in other eutrophized mangroves (e.g., Chen et al. 2010; Barroso et al. 2022).

In L + S tanks with crabs, leaves OM was incorporated to surface sediments (32% of the total SOM) although less than in the L tanks (Table 3) and the CO_2 fluxes were much lower than in the presence of crabs (Fig. 3). This observation was not aligned with previous findings of Kristensen and Alongi (2006) who measured higher CO_2 emissions from natural mangrove sediments with crabs burrows but with no continuous labile

OM input as the case in the L + S experiment. However, because our chambers were not specifically placed over the crab borrows, the CO_2 fluxes will not reflect the enhancement of gas and solute exchanges due to their presence, but only the impact of animal stepping and/or feeding activity on the mangrove floor. Lower CO_2 fluxes in the presence of crabs in L + S tanks (Fig. 3) suggests that crabs consumed a part of the labile OM which was available to microbes that contribute to CO_2 fluxes. This consumption of litter by crabs was confirmed by the higher concentration of Σ18PUFAs and EFAs, highly abundant in Mangroves leaves and *Sargassum* thalles, respectively, in their hepatopancreas compared to those reared in control tanks (Table 2).

Transfer of OC to subsurface sediments

During high tide, soluble compounds present in the mangrove leaves litter and embedded in surface sediments are leached (Steinke et al. 1993). Macrofauna such as crabs promote this leaching by mechanically fractionating the OM (Valiela et al. 1985). In the top layers, exposed to tidal drainage, redox oscillations favor remineralization of OM (Aller and Blair 2006). Conversely, OM may be partially stabilized by coprecipitation with metals and by sorption with the mineral substrate and is thus protected against remineralization (Kida and Fujitake 2020). During ebb and low tides, this OM percolates through the sediment and may reach the subsurface layer (Marchand et al. 2006).

Values of OC concentrations and $\delta^{13}C$ signatures of subsurface sediments were like those measured in surface sediments in all control and L tanks, with or without crabs (Table 3). In L tanks without crabs, only a little amount of leaves material, accumulated as litter on surface, was transferred toward the subsurface (Table 3). When present, crab consumption of leaves material limited the transfer of carbon toward the subsurface sediments (Table 3). This was consistent with results previously reported experimentally by Kristensen and Alongi (2006) that showed no influence of crabs on carbon content of subsurface sediments.

In L + S tanks without crabs, the OC concentration in subsurface sediments at T60 was 2 times higher than in the other treatments and SOM had a $\delta^{13}C$ signature close to that of mangrove leaves (Table 3). This reveals a significant transfer of surface OM derived from the leaves litter to deeper layers as also confirmed with almost 2–3 times more amounts of Σ18PUFAs at T60 compared to L treatment (Supporting Information Table S3). High concentrations of refractory OC such as tannin in mangrove leaves promote the formation of organometallic complexes, which could further enhance the sequestration of OM in the subsurface sediments (Costa et al. 2020). Organic carbon content of subsurface sediment in L + S tanks at T60 was more than three times higher than in the control (Table 3). Mangrove leaves contributed to more than 96% of this enrichment in the presence or absence of crabs. Contrary to mangrove leaves, *Sargassum* OM, was mainly degraded at surface, with a very little amount reaching the subsurface sediments either in presence or in the absence of crabs as revealed by the mixing model (4% and 0% of total OC, respectively, Table 3) as well by the very low amount of EFAs in subsurface compared to surface (Supporting Information Table S3).

Fiddler crabs enhanced the downward transfer of mangrove leave material by both mechanical fragmentation of the litter (Fig. 1) and by their preferential assimilation of labile *Sargassum* OM as shown by the three times higher EFAs concentrations in their hepatopancreas for those reared in the L + S tanks than those from the L and control tanks (Table 2).

Carbon budget and negative priming effect due to *Sargassum* beaching

The addition of easily decomposable labile OM to the sediment can accelerate remineralization of older SOM (priming effect) through an increase of microbial activity and a co-metabolism effect (Guenet et al. 2010b). Competition between SOM-degrading microorganisms and those who opportunistically consume labile OM produced by the partial degradation of refractory material also promotes the priming effect (Bianchi 2011). To grow, SOM-degrading microorganisms overproduce exoenzymes that degrade refractory compounds (Fontaine et al. 2003). Although the potential for priming effects is high in marine environments (Bianchi 2011), especially since eutrophication has become a major environmental concern (Barroso et al. 2022; Chynel et al. 2022), few studies have been conducted on its effects in coastal sediments. For instance, by measuring $\delta^{13}C$ of DIC and CO_2, Trevathan-Tackett et al. (2018) showed that the addition of seagrass leaves resulted in a net positive priming effect at surface SOM (0–1 cm).

Conversely, it has been reported that labile OM inputs could also slow down remineralization and/or stabilize the SOM, through a negative priming effect (Guenet et al. 2010a). This negative priming effect might be due to a switch in the metabolism of the microbial communities, which degrades the labile OM instead of the more refractory SOM (Lützow et al. 2006). Other experiments in marine and coastal sediments have reported that the addition of labile OM such as microalgae slows down SOM remineralization through a mechanism called "preferential substrate utilization" (Gontikaki et al. 2013; Trevathan-Tackett et al. 2018). Such a negative priming effect promoting stabilization of OC in the sediment was also the conclusion of Zheng et al. (2018) when showing that biochar (labile) inputs lead to increased incorporation of OM into the sedimentary prokaryotic biomass rather than remineralization. However, even if our data indicate a net negative effect and an enhancement of OC storage at the sediment sub-surface of the L + S tanks, we cannot rule out the possibility of some positive priming occurring on the SOM in the presence of *Sargassum*. Indeed, there was a higher bacterial biomass in surface and subsurface sediments compared to other treatments (i.e., BrFAs Fig. 4; Supporting Information Table S3), even if remineralization affected only a small proportion of the added OM (Fig. 2), and the 6–8 cm deep

layer became enriched in OC derived from leaf material (Table 3). In salt marsh sediments, Dinter et al. (2019) showed that the addition of glucose leads to a net positive priming effect when the sediments remain permanently drained, and to a priming effect slightly negative or null when the sediments are exposed to tidal conditions. These authors suggested that in sediments less subjected to seawater influence, prokaryotic communities switch to favor organisms with high biomass turnover (rapid growth and strong remineralization). Therefore, in the L + S tanks, the experimental reproduction of a tidal cycle may also have promoted the measured negative priming effect.

From the perspectives of our experimental findings, we may hypothesize that *Sargassum* massive and almost continuous beaching reported in west indies since more than a decade (Bernard et al. 2022) could enhance the accumulation in subsurface sediment of carbon derived from mangrove leaves through drastic change of microbiology of sediments. This accumulation of mangrove leaves carbon in subsurface sediments is even further increased by the natural activity of fiddler crabs that seem to feed well on *Sargassum*. which further promotes the negative priming effect. Fiddler crabs have therefore an effective role on blue carbon sequestration during *Sargassum* beaching event. Nevertheless, the efficiency of carbon storage enhancement potentially dependent from the intensity and frequency of *Sargassum* beaching, and massive and/or chronic *Sargassum* beaching and accumulation can also lead to mangrove mortality due to sulfide toxicity (Cobacho et al. 2024). For that reason, more research is necessary to document tipping points from enhanced net carbon storage, as in our mesocosm conditions, to net carbon loss in the case of mangrove tree mortality.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Conflict of Interest

None declared.

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