



Loss of POC and DOC on seagrass sediments by hydrodynamics

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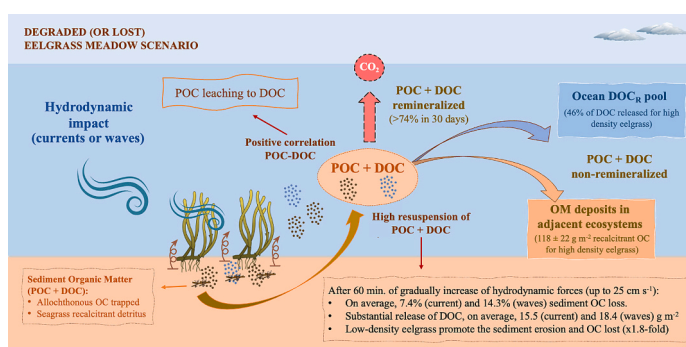
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HIGHLIGHTS

- Raise in hydrodynamic results in substantial release of DOC from surface sediments
- Low plant densities and leaf area result in higher OC resuspension ($\times 1.8$ -fold)
- Positive DOC-POC correlations suggest a high POC leaching to DOC.
- $>74\%$ of sediment-OC remineralized as CO_2 in 30 d.
- $\sim 118 \text{ g OC/m}^2$ (1 cm depth) remained after 30 day in high plant densities.

GRAPHICAL ABSTRACT



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ABSTRACT

Coastal development and climate change are sparking growing concern about the vulnerability of the organic carbon (OC) stocks in marine sediments to remineralization, especially in high threaten coastal ecosystems like seagrass meadows. Uncertainties still exist regarding the role played by hydrodynamics, seagrass canopies and sediment properties in OC resuspension and remineralization. A set of laboratory experiments were conducted to assess, for the first time, the mechanisms by which the particulate and dissolved organic carbon (POC and DOC) may be released and remineralized under hydrodynamic conditions (i.e., unidirectional and oscillatory flows) in two eelgrass densities and sediments properties (i.e., grain size and OC content). After a gradually increase in hydrodynamic forces, our results demonstrated that the presence of eelgrass reduced sediment erosion and OC loss in high-density canopies, while low-density canopies promote OC resuspension (on average, 1.8-fold higher than high-density canopies). We also demonstrated that unidirectional and oscillatory flows released similar DOC from surface sediments (on average, 15.5 ± 1.4 and $18.4 \pm 1.8 \text{ g m}^{-2}$, respectively), whereas oscillatory flow released significantly more POC than unidirectional flows (from 10.8 ± 1.1 to $32.1 \pm 5.6 \text{ g m}^{-2}$ for unidirectional and oscillatory flows, respectively). POC and DOC released was strongly influenced by both seagrass meadow structure (i.e., lower eelgrass density and shoot area) and sediment properties (i.e., lower mud and higher sediment water content). We found that, although $>74\%$ of OC in upper sediments was remineralized within 30 days, a relatively high amount of OC in high-density canopies is recalcitrant, highlighting its potential for the formation of blue carbon deposits. This study highlights the vulnerability of OC deposits in seagrass

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sediments to resuspension if the meadow is degraded and/or the climate change yield stronger storms, which could potentially weaken the seagrass meadows' service as blue carbon ecosystem in the future.

1. Introduction

Marine sediments are one of the larger and critical organic carbon (OC) reservoirs on the planet with an estimation of 2239–2391 PgC in the top 1 m, representing nearly twice that of terrestrial soils (Atwood et al., 2020), which makes them key for regulating climate change. Advances in human activities and climate change are sparking growing concern about the vulnerability of the C stocks in marine sediments to remineralization, a process that, furthermore, will likely exacerbate future climate change (Pendleton et al., 2012; Chen et al., 2022). Within marine ecosystems, vegetated coastal habitats rank among the most intense C sinks in the biosphere, being referred as blue carbon ecosystems (Mcleod et al., 2011). Globally, these habitats, including salt-marshes, mangrove swamps, seagrass and macroalgae meadows occupy 0.2 % of the ocean surface, but contribute significantly to ocean C sequestration (estimated ~50 % of OC in marine sediments; Duarte et al., 2013). Countries and states are increasingly looking to their blue carbon ecosystems as nature-based allies in the fight against climate change (Hilmi et al., 2021). However, the development of climate change mitigation strategies based on their protection and restoration, similar to those already existing for terrestrial ecosystems (e.g., Reducing Emissions from Deforestation and Forest Degradation Plus or REDD+ program), requires a robust understanding of the factors that may cause more resuspension and/or remineralization processes in sediment OC deposits (Chen et al., 2022).

Seagrasses are marine flowering plants that, despite its importance as blue carbon ecosystem (10–18 % of total C burial in the ocean; Mcleod et al., 2011), also rank among the most threatened marine ecosystems worldwide with increasing rates of meadows degradation and loss (Dunic et al., 2021). These high rates of meadow reduction concern about if they could shift from being a C sink to a C source by releasing vast amounts of stored OC from the sediment back into the ocean–atmosphere system (Moksnes et al., 2021; Piñeiro-Juncal et al., 2021). The above-ground structure formed by seagrass leaves and stems are known to substantially attenuate near-bed flows by exerting drag forces on the flow, decreasing the erosion and sediment resuspension (Infantes et al., 2012; Infantes et al., 2022). However, there is still a strong uncertainty about the role of the seagrass canopy and sediment properties in these processes (Fonseca et al., 2019; Schaefer and Nepf, 2022). For example, some studies have found that low or sparse canopy seagrass beds are capable of attenuating hydrodynamic forces (Potouroglou et al., 2017), meanwhile others studies have found that the protection against hydrodynamic processes might be lacking (Adhitya et al., 2014) or the effect could be the opposite, with increased turbulence around individual shoots (Dahl et al., 2018; Zhang et al., 2020). Furthermore, whereas the effect of unidirectional flows in this erosion and sediment resuspension has been well documented (e.g., Dahl et al., 2018) the effect of oscillatory flows (i.e., waves) is still one of the main gaps in the knowledge of the effects of hydrodynamic forces in seagrass, probably as a consequence of the technical complexity to generate waves in mesocosms (Infantes et al., 2021).

The OC in seagrass's sediments is composed by particulate (POC) and dissolved (DOC) organic carbon (Vichkovitten and Holmer, 2005). The DOC pool in seagrass sediments arises from the combination of OC from root exudates, since DOC is the main component of seagrass root exudation (Duarte et al., 2005), and leaching/decomposition of organic matter detritus (Liu et al., 2018). To date, the few studies about sediment erosion and the subsequent OC resuspension in seagrass meadows under oscillatory flows has been limited to POC fraction (Marin-Diaz et al., 2020; Barcelona et al., 2021), recording significant lower sediment erosion in seagrass meadow than in unvegetated sediments due to

the decrease in wave velocity and the turbulent kinetic energy by seagrass canopy. Nevertheless, its effect on DOC fraction remains unknown in spite that hydrodynamic forces has been highlighted as main factor in the DOC release from seagrass meadow, probably with a high contribution from sediment-derived DOC (Egea et al., 2018). A significant fraction of this DOC is formed by bioavailable material (also known as labile fraction), which is rapidly taken up by heterotrophic microbes (Navarro et al., 2004; Egea et al., 2019). Otherwise, another fraction of this DOC is less accessible to microbial degradation (also known as recalcitrant fraction) and it can be exported and sequestered in the deep ocean (Jiao et al., 2010; Duarte and Krause-Jensen, 2017; Jiménez-Ramos et al., 2022; Egea et al., 2023).

Once the OC is resuspended by higher hydrodynamic forces and/or seagrass meadow degradation, it is usually assumed that all the OC resuspended after seagrass loss it is entirely remineralized until CO₂, either in the area itself or in adjacent ecosystems where it may be deposited (Pendleton et al., 2012; Macreadie et al., 2014). However, this assumption still largely lacks empirical support (Moksnes et al., 2021). As vascular plants, seagrasses present complex aromatic structural biopolymers such as lignin (Vanholme et al., 2010), affecting the capacities of the microbial community to decompose seagrass debris (Trevathan-Tackett et al., 2017). Thus, although part of this resuspended OC can be remineralization as it becomes exposed to aerobic conditions (Piñeiro-Juncal et al., 2021), another part can be deposited again in adjacent ecosystems, given the nature of the organic matter in seagrass meadow and its refractory condition (Duarte and Krause-Jensen, 2017).

In this study, a set of laboratory experiments was designed to quantify (1) how much increasing hydrodynamic exposure (current and waves) can promote the export of POC and DOC? And (2) what is the potential of remineralization of OC stocks (i.e., the fraction that could be oxidized or transported elsewhere) in upper sediments of seagrass meadows? To answer these questions, we exposed sediment with two canopy densities of eelgrass and bare sediments to gradually increasing of unidirectional and oscillatory flow velocities in a hydraulic flume. This experimental setup allowed to assess the effects of canopy density and sediment properties on the export of POC and DOC. In parallel, we conducted an assay to estimate the bioavailability of C from the upper sediments to evaluate the potential of remineralization of OC stocks in these ecosystems. The obtained results will contribute to gaining more insights into the effects of hydrodynamic forces and seagrass degradation on the resuspension and remineralization processes of sediment organic matter, which ultimately will allow to predict the role of this ecosystem as blue carbon sink.

2. Materials and methods

2.1. Sampling sites

Sediment samples with the seagrass *Zostera marina* (eelgrass) and bare sediment were collected in two areas (i.e., Bokevik bay and Gåsö island) of the Gullmars Fjord on the Swedish Skagerrak coast (58°14'N, 11°26'E) near Kristineberg Marine Research Station. The sampling areas (3–10 m depth) were selected based on their natural variation in canopy density, i.e., from low- (LD) to high- (HD) density eelgrass, meanwhile the unvegetated sampling areas were select based on the sediment properties, i.e., from lower- (LC) to higher- (HC) carbon concentration sediments. Hence, four types of sediments were identified (Table 1). Samples were taken with a 0.35 m × 0.35 m box-core from a vessel and gently moved to custom-made trays of 0.35 m × 0.35 m placed underneath the box-corer. To keep the sediment structure intact, flat trays with the sediment were then placed in PVC boxes to protect the sediment

Table 1

Sediment features for each sediment sample tested. LC- and HC-unveg: lower- and higher-carbon concentration unvegetated sediments, LD- and HD-eelgrass: lower- and higher-density eelgrass sediments. AG and BG: above- and belowground eelgrass biomass, DW: dry weigh, Mud = grain size < 0.063 mm, OC and IC: sedimentary organic and inorganic carbon content, DBD: dry bulk density; β : water content. Different letters indicate significant differences among sediment type for each variable ($p < 0.05$).

Sediment type	Site	Shoot density (m ⁻²)	AG (gDW m ⁻²)	BG (gDW m ⁻²)	Mud (%)	OC (%)	IC (%)	DBD (g cm ⁻³)	β (%)	
Low C-unveg.	Gåsö	-	-	-	9.8	2.8	8.7	1.0	32	
		-	-	-	8.5	2.9	5.8	0.9	33	
		-	-	-	5.8	2.2	7.9	0.9	31	
		-	-	-	5.7	3.6	5.8	0.9	32	
		Mean \pm SE	-	-	-	7.4 \pm 1	2.9 + 0.3 ^a	7.1 + 0.7	0.9 \pm 0	32 \pm 0
High C-unveg.	Bokevik	-	-	-	12.3	6.1	9.9	0.8	28	
		-	-	-	10.7	4.0	7.4	0.8	33	
		-	-	-	8.6	6.3	6.2	0.9	33	
		-	-	-	12.3	5.3	8.4	0.6	63	
		-	-	-	9.2	6.3	8.8	0.8	53	
		-	-	-	11.7	4.3	7.6	0.8	51	
Mean \pm SE	-	-	-	10.8 \pm 0.7	5.4 + 0.4 ^b	8.1 + 0.5	0.8 \pm 0	43 \pm 6		
Low D-eelgrass	Bokevik	119	45.6	22.5	3.4	4.8	7.9	0.9	25	
		90	64.6	39.8	12.6	4.7	8.1	0.6	52	
		126	73.7	34.0	8.9	4.6	6.8	0.5	53	
		50	59.7	29.2	9.5	5.1	8.2	0.4	62	
		98	46.9	9.6	8.7	5.0	6.1	0.7	34	
		108	30.6	9.5	11.7	4.7	7.4	0.7	37	
		Mean \pm SE	98 \pm 11 ^a	53.5 \pm 6.3 ^a	24.1 \pm 5.1 ^a	9.1 \pm 1.3	4.8 + 0.1 ^b	7.4 + 0.3	0.6 \pm 0.1	44 \pm 6
High D-eelgrass	Gåsö	195	112.3	62.7	10.0	8.8	7.2	0.6	51	
		292	56.5	61.7	8.0	7.4	6.5	1.0	35	
		288	167.7	70.0	9.0	7.7	7.4	0.7	46	
		234	164.3	89.6	5.5	7.4	6.7	0.9	32	
		284	107.3	53.4	8.8	8.7	5.5	0.7	45	
		250	151.9	106.8	12.8	6.4	6.5	0.6	49	
		Mean \pm SE	257 \pm 16 ^b	126.7 \pm 17.5 ^b	74 \pm 8.2 ^b	9 \pm 1	7.7 + 0.4 ^c	6.6 + 0.3	0.7 \pm 0.1	43 \pm 3

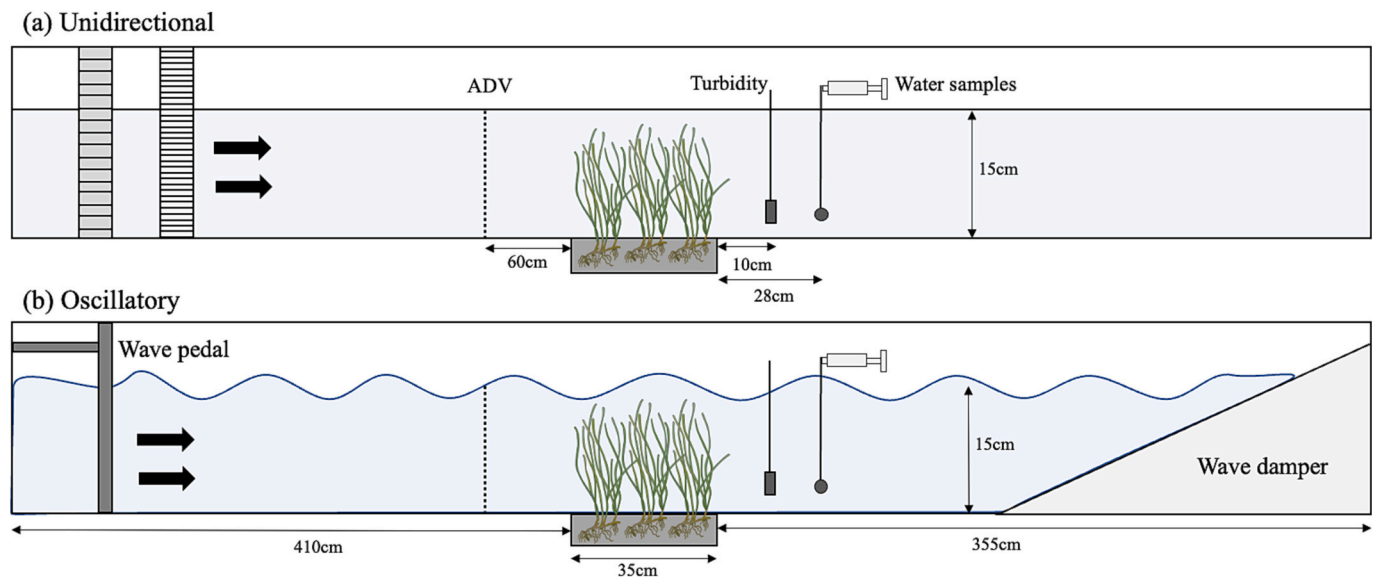


Fig. 1. Experimental setup for unidirectional and oscillatory flows in flume. a) unidirectional flow and b) oscillatory flow. Water depth was 15 cm. Dashed lines are the locations for the vertical profiles of flow velocity. Not drawn to scale.

from tilting during transport. In this way, sediment samples from the field were taken keeping the sediment properties and both aboveground and belowground biomass undisturbed (Dahl et al., 2018; Marin-Diaz et al., 2020). The sediment trays were placed in two tanks of 1000 L (1.5 \times 1.5 m) installed indoors at Kristineberg with similar seawater conditions than natural, i.e., salinity 33 PSU, temperature of 15 $^{\circ}$ C, light of 80 μ moles m⁻² s⁻¹, and a 12:12 h light/dark photoperiod, until trays were used in the hydrodynamic experiments.

2.2. Hydrodynamic flume

To assess the impact of hydrodynamic forces, unidirectional (i.e., current) or oscillatory (i.e., waves) flows, on the release of organic carbon (OC) from sediment samples, a hydraulic flume located at Kristineberg was used (Fig. 1). The flume was 8 m long, 0.5 m wide and 0.5 m depth and had a test section composed by a 0.35 \times 0.35 \times 0.15 m³ (length \times width \times height) cavity located in the middle of the flume. The flume was equipped with two separate flow generating systems, i.e., one for unidirectional and the other for oscillatory flow, enabling the application of different hydrodynamics forces required as needed.

Unidirectional flow velocities were generated by a motor-run propeller located at the far end of the flume. The propeller speed was controlled by an adjustable speed drive (Dayton Electronic, 6 K119). In the unidirectional flow setup, water was recirculated through a pipe installed at the base of the flume, where the propeller was also situated. For more technical details, see [Pereda-Briones et al. \(2018\)](#). Oscillatory flow velocities were generated by an electronic piston (Festo®) mounted on a rolling cart ([Infantes et al., 2021](#)). The wave amplitude and frequency of the waves were controlled by a computer program, allowing adjustment of the piston stroke and speed. A wave absorber made of synthetic fibers with a slope of 15° was placed at the end of the flume to reduce wave reflections.

To capture the unique flow characteristics of each regime, flow velocities were measured with an acoustic Doppler velocimeter, (ADV, Nortek, Vectrino) at a sampling rate of 25 Hz. Vertical profiles of velocity were measured at 5 positions (1, 2, 3, 5 and 7 cm above the bottom) located 60 cm before the test section. For unidirectional flow, the mean velocity was calculated to represent the average flow velocity. In contrast, for oscillatory flow runs, the mean orbital velocities (U_{rms} , cm s^{-1} ; Eq. (1)) were calculated as the mean fluctuating velocities over the oscillatory cycle,

$$U_{rms} = \sqrt{\frac{1}{N} \sum_{i=1}^n u_i^2} \quad (1)$$

where u is the horizontal flow velocity during n measurement points.

2.3. Hydrodynamic exposure

Twenty-two sediment samples ([Table 1](#)) were used to assess the effect of hydrodynamic forces on OC erosion and resuspension. One sediment sample and hydrodynamic force (i.e., unidirectional or oscillatory) were used for each test run, making two replicate runs for LC-unvegetated and three replicate runs for HC-unvegetated, LD-eelgrass and HD-eelgrass per hydrodynamic force, respectively. Depending on the type of hydrodynamics forces required for each run, the hydraulic flume was set up as it is explained in point 2.2. For each run, a sediment tray was carefully inserted in the test section of the flume and adjusted in order to be at the same level as the flume bottom. Then, the flume was filled up (440 L) with natural seawater from the fjord (ca. 33 PSU, ca. 13 °C) resulting in a fixed water depth of 0.15 m. This water depth did not entirely represent natural conditions but was adequate to simulate realistic bottom shear stress on the eelgrass canopies and surface sediments ([Infantes et al., 2021](#)). During each run, the sediment sample was exposed to four stepwise increases in current or orbital flow velocities, i.e., 5 cm s^{-1} , 10 cm s^{-1} , 17 cm s^{-1} , 25 cm s^{-1} , which is a common method used in hydraulic flumes to estimate erosion ([Jacobs et al., 2011](#); [Infantes et al., 2022](#)). Thus, the measures of particulate (POC; mg L^{-1}) and dissolved (DOC; mg L^{-1}) organic carbon obtained for each step and run is a cumulative value as gradually increase the flow velocity. The flow velocities selected represent similar current and wave exposures in shallow bays where eelgrass is present in the Swedish west coast ([Dahl et al., 2018](#); [Marin-Diaz et al., 2020](#)). Each flow velocity was run for 15 min before increasing the flow velocity (i.e., 1 h of current or waves exposure in total per run). Preliminary tests were conducted to determine the rate of OC diffusion as a result of samples manipulation. Although this OC loss was negligible, 15 min without flow was set at the beginning of each run to allow for the sediment to settle and subtract the diffusion of OC from sediment independently of hydrodynamics. Water turbidity was measured with YSI PRO DSS Multiparametric sensor, located 10 cm after the sample box and 5 cm above the bottom, recording data every 1 min. The sediment resuspension reached a steady state within the time frame of each velocity step, which was <15 min ([Fig. S1](#)). This time frame aligns with the findings of previous studies conducted under wave dominated regimes ([Oguz et al., 2013](#); [Ros et al., 2014](#)). wave dominated regime.

2.4. POC and DOC analysis in seawater

The particulate organic carbon (POC) and dissolved (DOC) organic carbon concentration from sediment erosion for each step velocity (i.e., 5, 10, 17 and 25 cm s^{-1}) within each run were measured by collecting a water sample at the end of each flow velocity step using a clear PVC syphoning tube introduced at the middle of the water column (~6 cm water depth) behind the test section (~28 cm from the center test section) to fill an acid-washed (5 days in 10 % HCl) and pre-combusted (5 h at 500 °C; for removing organic carbon) 0.6 L glass bottle. POC sample was taken by filtration of 0.5 L from the glass bottle through pre-weighed and pre-burned (for 2 h at 450 °C) Whatman GF/F filters. Then, the filters were dried for 48 h at 60 °C and re-weighed to quantify the concentration of sediment particles (mg L^{-1}) in the water column. DOC sample was taken by filling glass bottles (12 mL) through a 50 mL acid-washed syringe using pre-combusted (500 °C for 4 h) Whatman GF/F filters. Water samples were kept with 0.08 mL of H_3PO_4 (diluted 30 %) at 4 °C in acid-washed material (glass vials encapsulated with silicone-PTFE caps) until subsequently DOC analysis in laboratory. Concentrations of DOC (mg L^{-1}) were derived by catalytic oxidation at high temperature (720 °C) and chemiluminescence by using a Shimadzu TOC-VCPH analyser. DOC-certified reference material (Low and Deep), provided by D. A. Hansell and W. Chen (DSR: 44–45 of μM for DOC, University of Miami), were used to assess the accuracy of the estimations. The results were in good agreement with certified DSR values (deviation: <5 %).

To correct both the previous carbon content (i.e., POC and DOC) in the seawater and the possible DOC exchange between flume and the atmosphere, a control assay previous to the beginning of the experiment (i.e., flume filled with natural deep seawater but without sediment tray) were carry out to subtract the natural POC and DOC content in seawater during the run tests and the atmosphere-water DOC exchange effect. To correct the DOC released by seagrasses during the run tests, at the end of each run with seagrass samples, all the seagrass biomass (including belowground tissues) were gently moved to an aquarium filled with the same deep water and placed close to the flume in order to expose plants to same light and temperature conditions. The net DOC flux (i.e., the rate of change in DOC concentration between final and initial sample) was determined for the same time of experimental runs (i.e., 1 h) to subtract the DOC released by seagrasses during the run tests.

The DOC and POC export (g m^{-2} sediment surface) after each step and run (n) were estimated as:

$$POC(\text{g m}^{-2} \text{ sedi. surf.})_n = \frac{POC(\text{mg L}^{-1})_n \times VF(\text{L})}{\text{Sediment surface}(\text{m}^2)} \times \frac{\text{g}}{1000 \text{ mg}} \quad (2)$$

$$DOC(\text{g m}^{-2} \text{ sedi. surf.})_n = \frac{DOC(\text{mg L}^{-1})_n \times VF(\text{L})}{\text{Sediment surface}(\text{m}^2)} \times \frac{\text{g}}{1000 \text{ mg}} \quad (3)$$

where VF is the volume of the flume tank.

2.5. Sediments and meadow properties

The organic carbon content and sediment properties for each sediment sample were measured by collecting ~60 mL from the 0–1 cm sediment top layer before and at the end of each run using a cut-off syringe and dried at 60 °C for approximately 48 h. Dry bulk density (DBD) was calculated as the dry weight of the sediment divided by the volume of the original sediment sample. The percentage of water content of sediment (β) was determined as the difference between wet and dry sediment weight with respect wet weight.

Grain size was determined with a digital electromagnetic sieve shaker (FILTRA-2000). The grain size was measured using the dry-sieve method on a 100–150 g subsample of each soil core, to separate soil fractions along the Udden-Wentworth scale ([Wentworth, 1922](#)). The cumulative weights of grain size distribution data were used to calculate

median grain size (D_{50}) expressed in phi units, where $\phi = -\log_2 D$ (where D is particle diameter in millimeters). Samples were then ground to fine powder and homogenized and subdivided into two subsamples for organic carbon content (A-subsample) and inorganic carbon content (B-subsample). The measurement of carbon content in the sediments samples was performed at the Institute of Marine Research (INMAR) at University of Cádiz (Spain), following the procedures described by Howard et al. (2014). Total carbon (and nitrogen) content (%) were measured in ca. 0.15 g dry weight of A-subsample through an automated elemental analyser (LECO CNS928). Inorganic carbon content (%) was determined in ca. 1 g of dry weight from B-subsamples using the acidification method with HCL 1 N (Howard et al., 2014). Then, the organic carbon content (OC, %) was calculated as the difference between the total and inorganic carbon (Howard et al., 2014). The sediment and organic carbon and nitrogen densities (g cm^{-3}) were calculated from the total dry weight of the sediment samples, including belowground biomass fragments, stones and shells, as this constitutes a part of the sediment and the sediment volume (although to a minor extent).

Regarding isotopes analyses, after removal of inorganic carbon by addition of 1 N HCl (Kennedy et al., 2005) in sediment samples, subsamples of 10 mg DW were used for elemental and isotopic determination using a ratio mass spectrometry-elemental analyser at the SAI laboratories (A Coruña University, Spain). Stable isotope ratios were converted to ‰ notation using Vienna Pee Dee Belemnite (VPDB) and air- N_2 as standards for C and N, respectively. The relative contribution of the potential sources (i.e., endmembers) to the pool of surface sediment OM was explored using Stable Isotope Bayesian mixing models ("simmr" R package; Parnell, 2019). The models were run using the $\delta^{13}\text{C}$ (from the organic fraction) and $\delta^{15}\text{N}$ (from the total fraction) signatures of the sediment ($n = 4$ of each sediment type) and the same signature of the 4 endmembers: leaves ($n = 8$) and rhizomes ($n = 8$) of eelgrass, pool of macroalgae present in the area (mix of *Fucus* spp., *Ulva intestinalis* and *Chorda filum*) ($n = 8$) and POM in water column (i.e., seston; $n = 6$). Endmember $\delta^{13}\text{C}$ values and N/C ratios are reported in supplementary information (Table S1). The mean and standard deviations of isotopic signatures for those sources were obtained from samples collected in the area of study (Güllmars Fjord). Results of the mixing models, either in the upper sediment samples before and after the bioavailable assay (explained at point 2.6), were given as theoretical contribution (%) of each source to the sedimentary OM pool (mixtures).

The initial top 1 cm organic and inorganic carbon content (respectively OC and IC stock) of each sediment sample were calculated as

$$OC_{stock}(g) = DBD(\text{g cm}^{-3}) \times OC(\%) \times SS(\text{cm}^3)/100 \quad (4)$$

$$IC_{stock}(g) = DBD(\text{g cm}^{-3}) \times IC(\%) \times SS(\text{cm}^3)/100 \quad (5)$$

where SS is the sediment slice obtained as the sediment sample area \times 1 cm depth.

The total organic carbon lost from surface sediments (top 1 cm) (TOC) after each step and run (n) were estimated as:

$$TOC_n(\%) = \frac{[POC_n(\text{mg L}^{-1}) + DOC_n(\text{mg L}^{-1})] \times VF(L) \times \frac{g}{1000\text{mg}}}{OC_{stock}(g)} \times 100 \quad (6)$$

where VF is the volume of the flume tank.

The suspended inorganic sediment concentration (SIS) after each step and run (n) were estimated as:

$$SIS(\text{g m}^{-2} \text{ surf. sedi.})_n = \frac{[STS_n(\text{mg L}^{-1}) - TOM_n(\text{mg L}^{-1})] \times VF(L)}{\text{Surface sediment}(\text{m}^2)} \times \frac{g}{1000\text{mg}} \quad (7)$$

where STS is the suspended total sediment, TOM is the total organic matter and VF is the volume of the flume tank.

After each run, the seagrass biomass, plant morphology and shoot density ($\text{n}^\circ \text{m}^{-2}$) were measured. To calculate the biomass, plants were rinsed, dried at 60 °C and weighed to estimate the photosynthetic (AG-aboveground) and the subterranean (BG-belowground) biomass (dry weight; g DW m^{-2}). Before drying, three randomly shoots were selected within three representative sediment vegetated samples from each sampling site (i.e., Bokevik bay and Gåsö island; $n = 9$) to estimate the number of leaves per shoot (leaves shoot $^{-1}$), leaf length (including basal sheath; cm), width (using calipers in the middle of each leaf; cm) and leaf area per shoot ($\text{cm}^2 \text{ shoot}^{-1}$).

2.6. Assay to estimate the bioavailability of C stock from upper sediments

Sediment samples (60 mL) were collected from the top 1 cm surface and were exposed during 30 days to high remobilization (through aeration), O_2 conditions and dark in order to assess the bioavailability of OC deposits (i.e., POC and DOC) to estimate the risk of remineralization of resuspended sedimentary OC deposits. It should be noted that we use the term bioavailable (i.e., accessible to microbial degradation) as the OC which is used by heterotrophic microorganism within days, according to previous studies on degradation rates of OC (e.g., Jiménez-Ramos et al., 2022). Six replicates glass bottles (750 mL) per sediment type (i.e., LD-eelgrass, HD-eelgrass, LC-unvegetated and HC-unvegetated) were used as incubations ($n = 24$) filled with sediment samples (60 mL) and artificial seawater (440 mL) (Pro-Reef Meersalz/Sea Salt) with a similar origin salinity from in situ areas (33 PSU) and negligible DOC concentration. Air stones (40 \times 40 mm) were setting to incubations to provide oxygenation and ensure adequate mixing of water. OC bioavailability assays were run until mixed microbial communities reached stationary phase (<30 days) in a temperature-controlled room set at 18 °C and darkness conditions (Jiménez-Ramos et al., 2022). Ammonium (NH_4Cl) and phosphate (NaH_2PO_4) concentration were maintained to 10 and 0.7 μM respectively (minimum concentration in experimental area; Wesslander et al., 2018) during experimental period, to avoid growth limitation by either nitrogen or phosphorus availability. One replicate of each sediment type was retrieved for DOC and bacterial abundance at 6 different sampling times on day 0, 4, 10, 16, 23 and 30. For DOC samples, triplicate samples of water (10 mL) were collected and measured as it was indicated in Section 2.4. For bacterial samples, triplicate samples of water (1.5 mL) were collected and fixed immediately with cold 10 % glutaraldehyde (final concentration, 1 %), left in the dark for 10 min at room temperature and then, stored at -80 °C. Bacterial abundance was counted with a FacsAriaII (Cell Sorter) flow cytometer as described previously in Gasol and Del Giorgio (2000). On the other hand, sediment samples were collecting in each incubations at initial day and at the end of incubation time (30d) to calculate POC concentration (pool of three subsamples of homogenized sediment following same methodology in Section 2.5). Moreover, at 30th day samples (end of assay), one subsample of 10 mg DW of each sediment type was also collected to isotope analyses (see methodology in Section 2.5).

2.7. Data and statistical analyses

Differences among sediment types (i.e., LC-unvegetated, HC-unvegetated, LD-eelgrass and HD-eelgrass) hydrodynamic exposure (i.e., unidirectional and oscillatory flow), flow velocity (i.e., 5, 10, 17 and 25 cm s^{-1}) and sediment fraction (i.e., POC and DOC) on each response variable were tested using generalized linear models (GLMs). The GLMs included fixed factors, as well as the interaction between the factors. For each response variable, we selected a particular family error structure and link function to reach the assumptions of linearity, homogeneity of variances and no overdispersion, which were checked through visual inspection of residuals and Q-Q plots (Harrison et al., 2018) after modelization. Sediment features (mud content, organic and inorganic carbon content, DBD and water content) and eelgrass characteristics

(shoot density, AG- and BG-biomass, length and width of leaves and number of leaves per shoot) were modelled using Gaussian distribution with identity link. POC and DOC concentrations, total OC lost and SIS were modelled using Gamma distribution with inverse link. Pairwise comparisons were tested using estimated marginal means with a Bonferroni correction (“emmeans” R package, Lenth et al., 2019). Correlation between DOC and POC and between those with flow velocities were tested using linear models. Assumptions of normality and homoscedasticity were assessed through examination of the residuals of all linear models. DOC bioavailability results were modelled by generalized additive models (GAMs) using the R package “mgcv” with time as random factor. Model selection was performed under the Akaike's Information Criterion (AIC), allowing the selection of the most parsimonious model (Wood, 2017). The GAMs were generated with a Gamma distribution, an inverse link function, a cubic regression spline and a smoothing parameter ($k = 4$). Statistical analyses were computed with R statistical software 4.2.0 (R Development Core Team, 2022). Data are presented as mean \pm SE.

3. Results

3.1. Description of sediment features and seagrass canopy

The unvegetated sediments from Bokevik (i.e., HC-unvegetated) and vegetated sediments from both locations (i.e., Bokevik or LD-eelgrass and Gåsö or HD-eelgrass) showed similar sediment composition, whereas unvegetated sediments from Gåsö (i.e., LC-unvegetated) showed significant lower OC and mud content and a tendency toward lower water content (26 % lower than the average of other three sediment types, respectively; Tables 1 and S2). Leaf length, width and number of leaves per shoot were significantly higher in HD-eelgrass (Table S3). Vegetated sediments showed similar mud content, DBD and water content but sediments from HD-eelgrass exhibited significantly higher OC content (Table 1). The sediment grain-size distributions were similar regardless of the sediment type studied (Fig. S2). On average, the median diameter (D_{50}) was ca. 170 classified as “fine sand”.

The range of stable isotope signatures of the sediment OM were within the ranges of the sources' signatures (leaves and rhizomes of eelgrass, pool of *Fucus* spp., *Ulva intestinalis* and *Chorda filum* macroalgae species present in the area and POM in water column -i.e., seston-), allowing to calculate the theoretical contribution of the sources to the sedimentary OM pool with the mixing model. The mixing model results

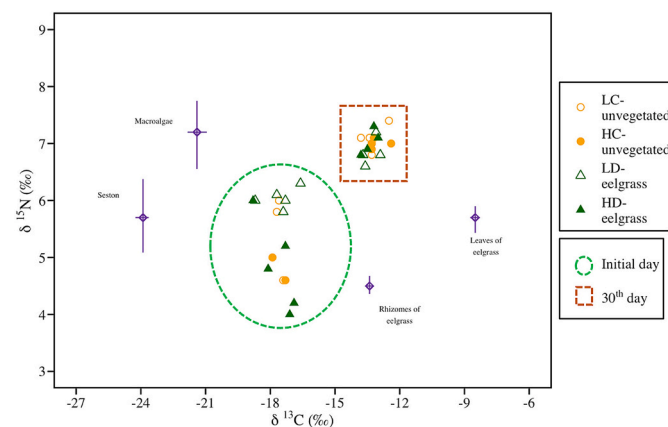


Fig. 2. Isotopic signatures of sedimentary organic matter and sources. Isotopic signatures $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of the sedimentary organic matter pool at the beginning of runs and after 30 days of bioavailable assay, and signatures of organic matter sources (mean \pm standard deviation). LC- and HC-unvegetated: lower- and higher-carbon concentration unvegetated sediment, LD- and HD-eelgrass: lower- and higher-density eelgrass.

revealed that the microbial communities studied had a mix of autochthonous (i.e., from seagrass tissues) and allochthonous (i.e., from macroalgae and seston) carbon source (Figs. 2 and S3). Notable correlations were observed between leaves and rhizomes of eelgrass, making difficult separability in terms of isospace. The proportions were similar among sources (~ 25 % on average) in unvegetated sediments, meaning that no single source was clearly identified as being dominant. Pool of *Fucus* spp., *Ulva intestinalis* and *Chorda filum* macroalgae species were the main contributor (~ 40 % on average) of the sedimentary OM in LD-eelgrass, meanwhile rhizomes and seston were the main contributors (~ 30 % and ~ 35 % on average respectively) of the sedimentary OM in HD-eelgrass. After bioavailable assay (i.e., 30 days exposing the sediment samples to high remobilization, O_2 conditions and dark) the proportion of all the OM sources decreased except the leaves of eelgrass that increased (representing between 50 and 60 % on average) in all sediment types analysed.

3.2. Analysis of sediment resuspension and DOC export

There was a positive relationship between the increase in hydrodynamic forces, both unidirectional and oscillatory flows, and OC release from sediment samples, either particulate (POC) and dissolved (DOC) forms (Fig. 3, Tables S4 and S5). After 60 min gradually increase of hydrodynamic forces, oscillatory flow released significantly more POC than unidirectional flows (on average, 2.9-fold higher, from 10.8 ± 1.1 to 32.1 ± 5.6 g POC m^{-2} surface sediment under unidirectional and oscillatory flow, respectively). By contrast, unidirectional and oscillatory flows released similar DOC from surface sediments (on average, 15.5 ± 1.4 and 18.4 ± 1.8 g DOC m^{-2} , respectively). The POC released varied significantly among sediment types at high velocities under both hydrodynamic forces. LD-eelgrass sediments showed the highest POC resuspension at the highest flow (i.e., 25 cm s^{-1}) either under unidirectional and oscillatory flow (13.9 ± 2 and 44.8 ± 7.3 g m^{-2} sediment surface, respectively). By contrast, the HD-seagrass sediments showed a smoother POC release with the increase in hydrodynamic forces, being significantly lower than POC released from LD-eelgrass sediments at the highest flow. Regarding DOC export, the increase in hydrodynamic forces triggered higher DOC release from all sediment, with HD-eelgrass sediments showing the lower DOC release (11.7 ± 1.8 and 16.6 ± 6.0 g m^{-2} sediment surface for unidirectional and oscillatory flow respectively) although non-significant differences were found among sediment types.

Positive correlations between DOC and POC were found under unidirectional flow (linear model, $r^2 = 0.46$ and $R^2 = 0.57$, $p < 0.001$, for unvegetated- and eelgrass-sediments respectively). By contrast, under oscillatory flow, the positive correlations were only found for unvegetated sediments (linear model, $r^2 = 0.6$, $p < 0.001$, Fig. 4).

The total organic carbon (TOC) lost from surface sediment (top 1 cm) were significantly higher under oscillatory flow than under unidirectional flow at higher flow velocities (i.e., at 17 and 25 cm s^{-1}) for both unvegetated (general linear model, $\text{SE} = 1.65$, t -value = 2.63 , $p = 0.01$) and eelgrass-vegetated sediments (general linear model, $\text{SE} = 0.07$, t -value = -2.42 , $p < 0.02$) (Fig. 5a, b). The flow velocity raise significantly increased the TOC lost (%) from surface sediments (top 1 cm) in both unvegetated sediments analysed (Fig. 5a, b, Table S6), being on average, 3-fold (unidirectional) and 4-fold (oscillatory) higher at 25 cm s^{-1} respect 5 cm s^{-1} , and in seagrass-vegetated sediments, being on average, 2.9-fold (unidirectional) and 5.2-fold (oscillatory) higher at 25 cm s^{-1} respect 5 cm s^{-1} . The suspended inorganic sediment concentration (SIS) was significantly higher under oscillatory flow than under unidirectional flow. The flow velocity raise, either unidirectional and oscillatory, significantly increased the resuspension of SIS in both unvegetated and eelgrass-vegetated sediments (Fig. 5c, d, Table S6).

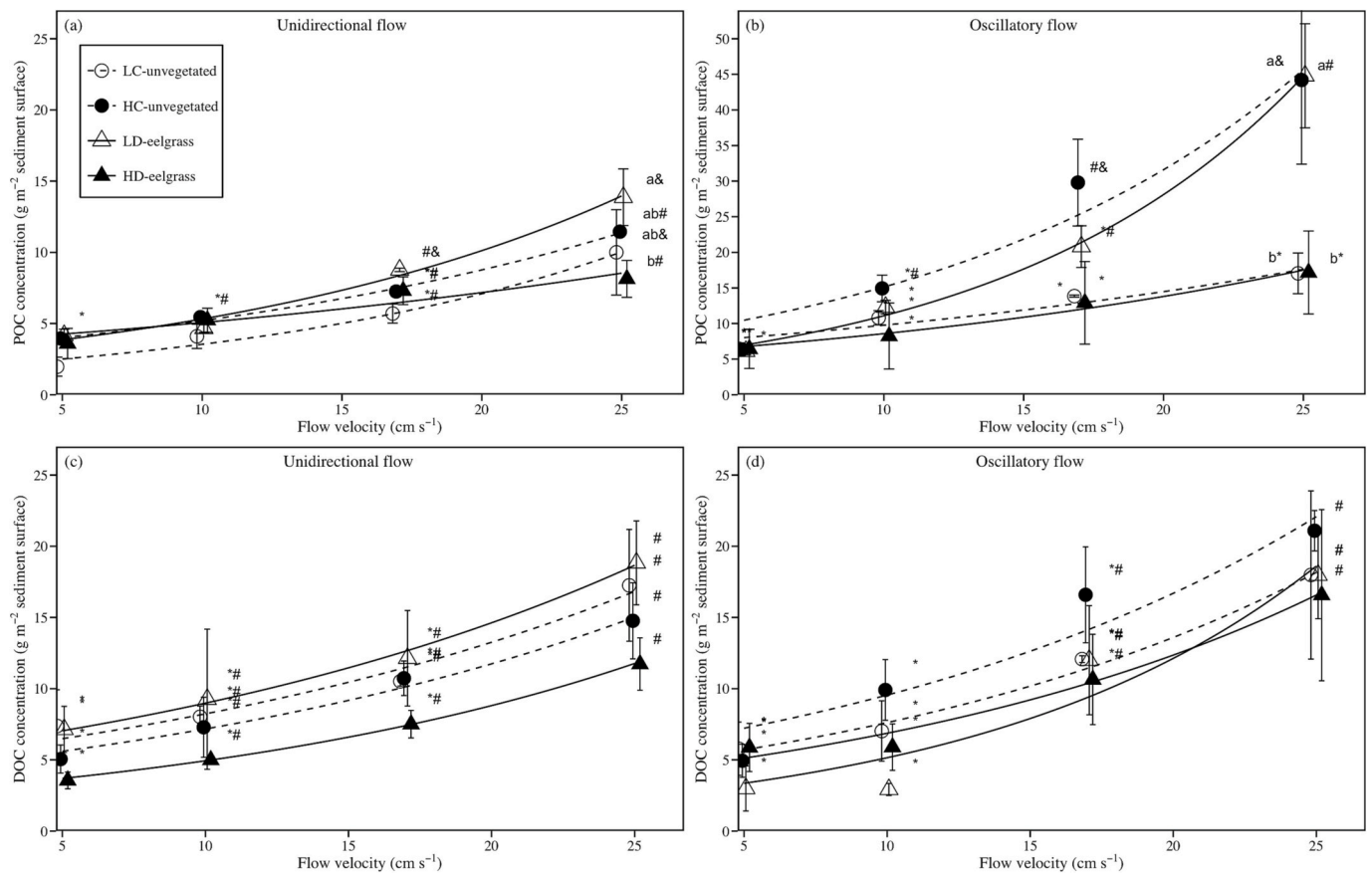


Fig. 3. Effect of flow velocities on POC and DOC concentrations in different sediment conditions. Unidirectional and oscillatory flow velocities on (a, b) suspended particulate carbon (POC) and (c, d) suspended dissolved carbon (DOC) concentrations. LC- and HC-unvegetated: lower- and higher-carbon concentration unvegetated sediment, LD- and HD-eelgrass: lower- and higher-density eelgrass. Lines show the GLMs fitted to each sediment type. Letters (ab) indicate significant differences among sediment types that are independent of flow velocities, while symbols (*#&) indicate differences among flow velocities that are independent of sediment types. Scale differs in Y-axis for b plot.

3.3. Assay to estimate the bioavailability of C stock from upper sediments

All microbial communities exhibited a high OC decay rates (>74 % in 30 days) for the surface sediments (top 1 cm) indicating a high proportion of labile material. HD-eelgrass sediment showed the highest initial OC stock, 2-fold higher than those in unvegetated sediments and LD-eelgrass sediment. After 30 days expose to high remineralization, oxic conditions and dark, the highest OC remained in HD-eelgrass sediment, (on average, 2.1-fold and 1.8-fold higher than those in unvegetated and LD-eelgrass respectively; Tables 2a and S7). Regarding DOC release, a sharp increase in the DOC concentration occurred during the first period (i.e., until 10th day) of high remineralization condition exposure (Fig. 6). Unvegetated sediments and sediments from LD-eelgrass canopies reached the DOC peak concentration at 4th day, meanwhile sediments from HD-eelgrass canopies reached it at 10th day. The increase was especially marked in LC-unvegetated. After those increases, DOC concentration showed a marked decrease until 30th day in all sediment types. Then, DOC concentration exhibited a plateau phase in all sediments. The labile fraction of DOC (i.e., DOC_L or DOC consumption from DOC peak to DOC at plateau phase) was significantly higher in unvegetated sediments, whereas the recalcitrant fraction of DOC (DOC_R or remained DOC at plateau phase) was significantly higher in eelgrass-vegetated sediments, showing the highest DOC_R in the HD-eelgrass canopies (Tables 2b and S7).

4. Discussion

4.1. Loss of POC and DOC from upper sediments by hydrodynamics

The gradual increase in hydrodynamic forces assessing in this study (i.e., either unidirectional and oscillatory flows) evidenced a significant erosion of sediments, in turn leading to the release of both stored organic and inorganic carbon, and hence the loss of the seagrass meadows' ability to sequester carbon. The laboratory set-up represented field conditions with flow velocities representing shallow coastal areas with a short fetch where seagrass usually thrive (Dahl et al., 2020; Infantes et al., 2021). Both unidirectional and oscillatory flows released similar DOC from surface sediments, whereas oscillatory flow released significantly more POC than unidirectional flows in all sediment types and flow velocities (Fig. 3). The presence of eelgrass yielded opposite responses depending on canopy density. Overall, the resuspension of POC were significantly lower in the HD-eelgrass than in LD-eelgrass, in both hydrodynamic treatments. Likewise, a tendency to lower DOC export were found in HD-eelgrass, although non statically differences were reached. The relatively low canopy density in both eelgrass meadows (average of 98 ± 11 and 257 ± 16 shoots m^{-2} in LD- and HD-eelgrass respectively, whereas those for another spots of Baltic Sea is 417 shoots m^{-2} ; Röhr et al., 2016) probably weak the protection against a horizontal flow, as it also has been observed in previous works with low-shoot density (e.g., Adhitya et al., 2014). In addition, the low plant density could also increase the turbulence and scouring around individual shoots as flow moves through the sparse canopy (Bouma et al., 2009; Marin-Diaz et al., 2020). This would explain both, the higher OC

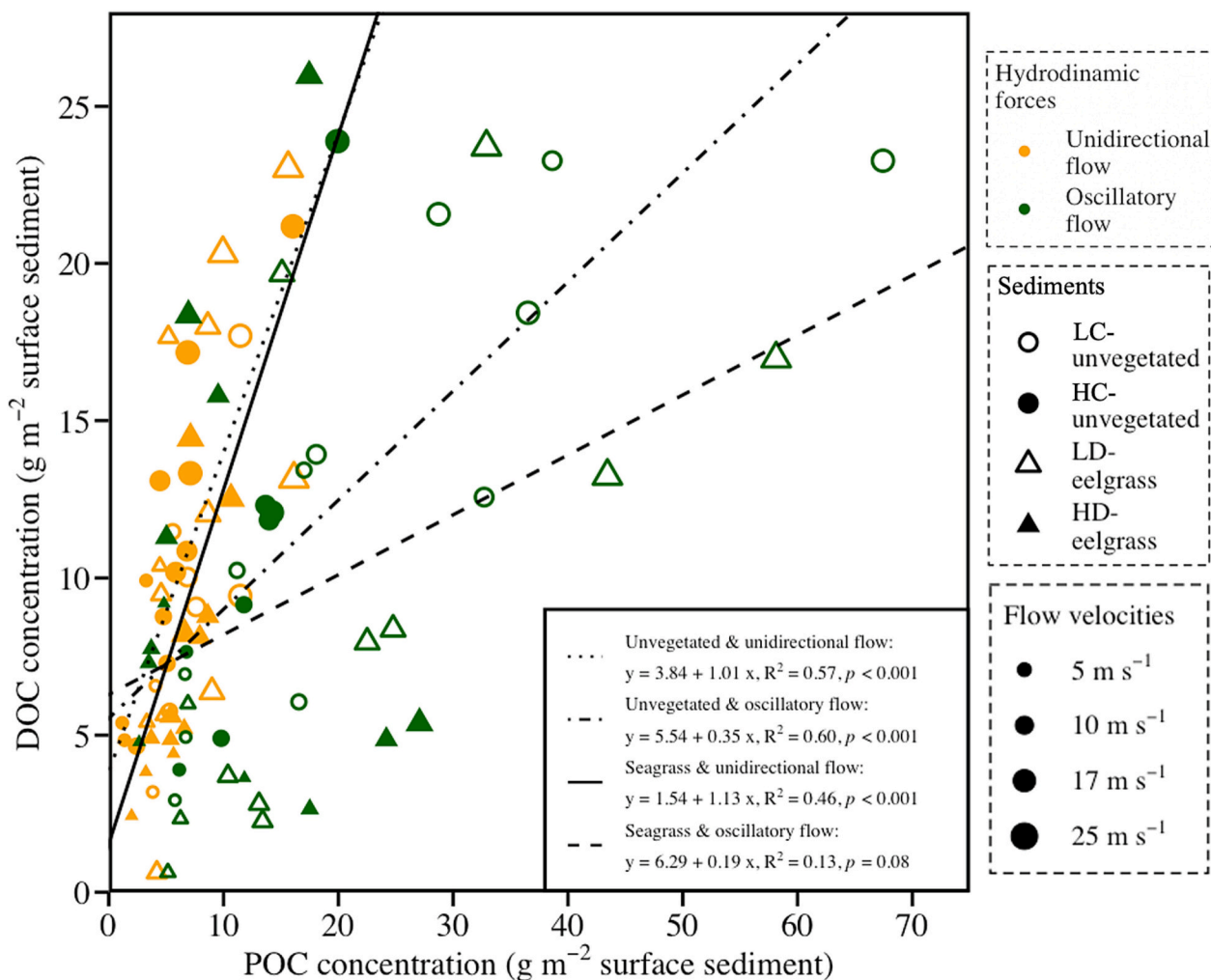


Fig. 4. Correlations between suspended dissolved- (DOC) and suspended particulate- (POC) OC concentrations. Lines represent the DOC-POC correlations for the combinations of sediment types and hydrodynamic forces. LC- and HC-unvegetated: lower- and higher-carbon concentration unvegetated sediment, LD- and HD-eelgrass: lower- and higher-density eelgrass.

release in the LD-eelgrass and the non-significant difference among HD-eelgrass and unvegetated sediments (Fig. 3). Regarding the effect of sediments features, unvegetated sediments with low percentage of water content (i.e., from Gåsö; $\beta = 32.1 \pm 0.4$) showed significantly lower release of POC than unvegetated sediments with high percentage of water content (i.e., from Bokevik; $\beta = 43.4 \pm 5.7$), especially under oscillatory fluxes. As the water content decrease, the specific weight of the sediment increase yielding changes the state of the sediment from fluid to solid phase (Jacobs et al., 2011) and limiting the OC loss under hydrodynamic exposure conditions.

The present study demonstrates that the raise in hydrodynamic forces, not only results in a higher POC release from surface sediments (Dahl et al., 2018), but it also results in substantial release of DOC, similar to the POC release under unidirectional flows (general linear model, SE = 0.057, t -value = 1.31, $p = 0.194$). Part of this DOC likely originates from the previous DOC stock present in the sediment (DOC_{SPS}), which is composed of DOC from root exudation in seagrass sediments (Duarte et al., 2005) and the leaching/decomposition of organic matter detritus (Liu et al., 2018). As the hydrodynamic conditions intensify and disturb the sediment–water interface, the concentration gradient of DOC in the sediment pore water decreases, potentially leading to the release of DOC_{SPS} (Burdige et al., 1992; Adhitya et al., 2016). However, previous studies have shown rapid leaching of DOC from the degradation of macrophytes biomass, such as within 15 min in Castaldelli et al. (2003). This finding led us to

hypothesize that another portion of the DOC may originate from the rapid leaching of resuspended POC (DOC_{LRP}) under oxic conditions (Lavery et al., 2013; Liu et al., 2018). Unfortunately, due to the complexity of the experimental design employed in this study, we were unable to collect time–course samples at each velocity step using benthic incubations. Such an approach would have been necessary to distinguish between DOC_{SPS} and DOC_{LRP} (e.g., Lavery et al., 2001; Maher and Eyre, 2010). This aspect should be considered in future experiments to clarify the origin of the increased concentration of DOC observed with the intensification of hydrodynamics disturbances.

The positive relation between DOC flux and higher velocities flows can be attributed to the sum of different processes. First, as the flow velocities increase, the vibration loads inducing by higher incipient velocity boosting the diffusive flux of the DOC already stored under layers of sediments (Rühl et al., 2020). Second, potential transformation of POC into DOC. The sharp increase in the DOC concentration found in the assay to estimate the bioavailability of C stock from upper sediments (Fig. 6) and the positive correlation between DOC and POC (Fig. 4) found in this study suggest a high POC leaching to DOC, as noted in previous works (Hoikkala et al., 2012; Maciejewska and Pempkowiak, 2014). Third, the raise in flow velocity enhance the gross primary production (GPP) of seagrasses (Egea et al., 2018), and since a part of the GPP is released as DOC (Jiménez-Ramos et al., 2023), increasing flow velocities indirectly results in a higher release of DOC. This has important ecological implications, since the labile fraction of DOC is quickly

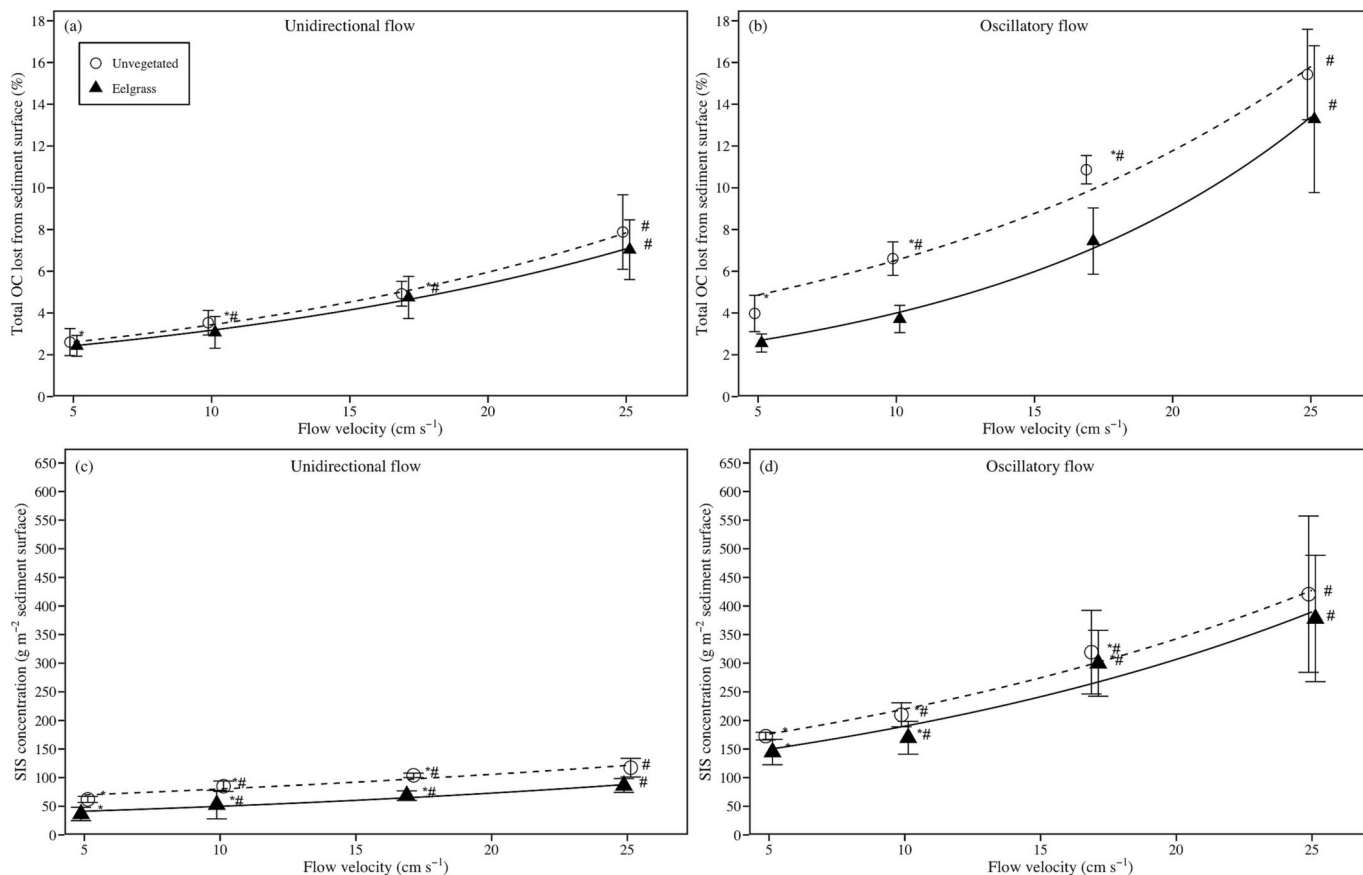


Fig. 5. Flow velocity effects on OC loss and sediment concentration in seagrass sediments. The percent of OC lost in seagrass-vegetated and unvegetated sediments (mean \pm SE) from surface sediment (top 1 cm) at different flow velocities for (a) unidirectional and (b) oscillatory flow. The suspended inorganic sediment concentration (SIS; g m^{-2} sediment) in eelgrass-vegetated and unvegetated sediment at different flow velocities for (c) unidirectional and (d) oscillatory flow. Lines show the GLMs fitted to seagrass-vegetated and unvegetated sediments, respectively. Symbols (*#) indicate differences among flow velocities that are independent of sediment types. Scale differs in Y-axis.

Table 2

OC stock at initial and final of the bioavailability C assay and concentrations of labile and recalcitrant fractions of DOC. LC- and HC-unveg: lower- and higher-carbon concentration unvegetated sediment, LD- and HD-eelgrass: lower- and higher-density eelgrass. DOC_L : labile fraction of DOC; DOC_R : recalcitrant fraction of DOC; DW: dry weight. Different letters indicate significant differences between sediment types.

(a)	Initial OC ($\text{mg}\cdot\text{g DW sediment}^{-1}$)	Final OC ($\text{mg}\cdot\text{g DW sediment}^{-1}$)	OC decay rate (%)
LC-unveg.	26.3 \pm 2	7 \pm 4.3	74 \pm 5 ^a
HC-unveg.	50.6 \pm 10.6	6 \pm 12.7	88 \pm 2 ^b
LD-eelgrass	47.8 \pm 0.5	10.3 \pm 0.8	78 \pm 2 ^{ab}
HD-eelgrass	81.1 \pm 7.2	15.8 \pm 2.9	81 \pm 4 ^{ab}

(b)	DOC_L (mg L^{-1})	DOC_R (mg L^{-1})	DOC_R (%)
LC-unveg.	253.6 \pm 7.8 ^a	42.9 \pm 5.9 ^{ab}	14 \pm 1 ^a
HC-unveg.	125.8 \pm 10.3 ^b	29.3 \pm 5.3 ^a	19 \pm 4 ^a
LD-eelgrass	102.9 \pm 3.1 ^{bc}	49.6 \pm 3 ^b	32 \pm 2 ^b
HD-eelgrass	84.9 \pm 4.5 ^c	72.6 \pm 0.9 ^c	46 \pm 1 ^c

consumed by microorganisms (lifetime average \sim 0.001 years; Hansell, 2013), thus acting as a transfer of carbon in the food web and as an essential carbon exchange pathway among communities (Navarro et al., 2004; Egea et al., 2019). However, the recalcitrant fraction of DOC (lifetime average \sim 1.5–40,000 years; Hansell, 2013) is resistant to rapid microbial degradation, being accumulated and sequestered in

continental shelf sediments or in the deep sea, and therefore contribute to carbon sequestration (Duarte and Krause-Jensen, 2017; Jiménez-Ramos et al., 2022; Egea et al., 2023).

4.2. Evaluating the bioavailability of OC stock from upper sediments

All sediment types exhibited a high OC decay rates ($>74\%$ within 30 days; Table 2) indicating a high potential of soil OC remineralization from degraded or lost seagrass meadow. The methodology used here was similar to previous studies on OC degradation (e.g., Sitterley et al., 2021; Jiménez-Ramos et al., 2022) but it also involved some limitations. The growth and structure of the bacterial community may be altered during a confined incubation (i.e., “bottle effect”; Massana et al., 2001). In addition, some previous studies indicated that short-term degradation experiments may underestimate the long-term persistence of OC (e.g., Trevathan-Tackett et al., 2020). Finally, there are processes that were not measured in this study (e.g., photochemical degradation, anaerobic metabolism, etc.). However, since a stationary phase in OC concentration was reached at the end of the bioassay, the possible artifacts introduced by our experimental setup are considered negligible as it would hardly modify the trends found in the experiment (i.e., high potential of OC remineralization from resuspended seagrass sediments). As seagrass detritus tend to be highly recalcitrant due to a low nutritional value and the more refractory nature of below-ground tissues (Trevathan-Tackett et al., 2017), it would be expected a lower OC decay rates. However, since eelgrass is a relatively small seagrass specie with relatively low below-ground biomass (Lavery et al., 2013), most of the OC sequestered is of allochthonous origin and thus relatively labile and

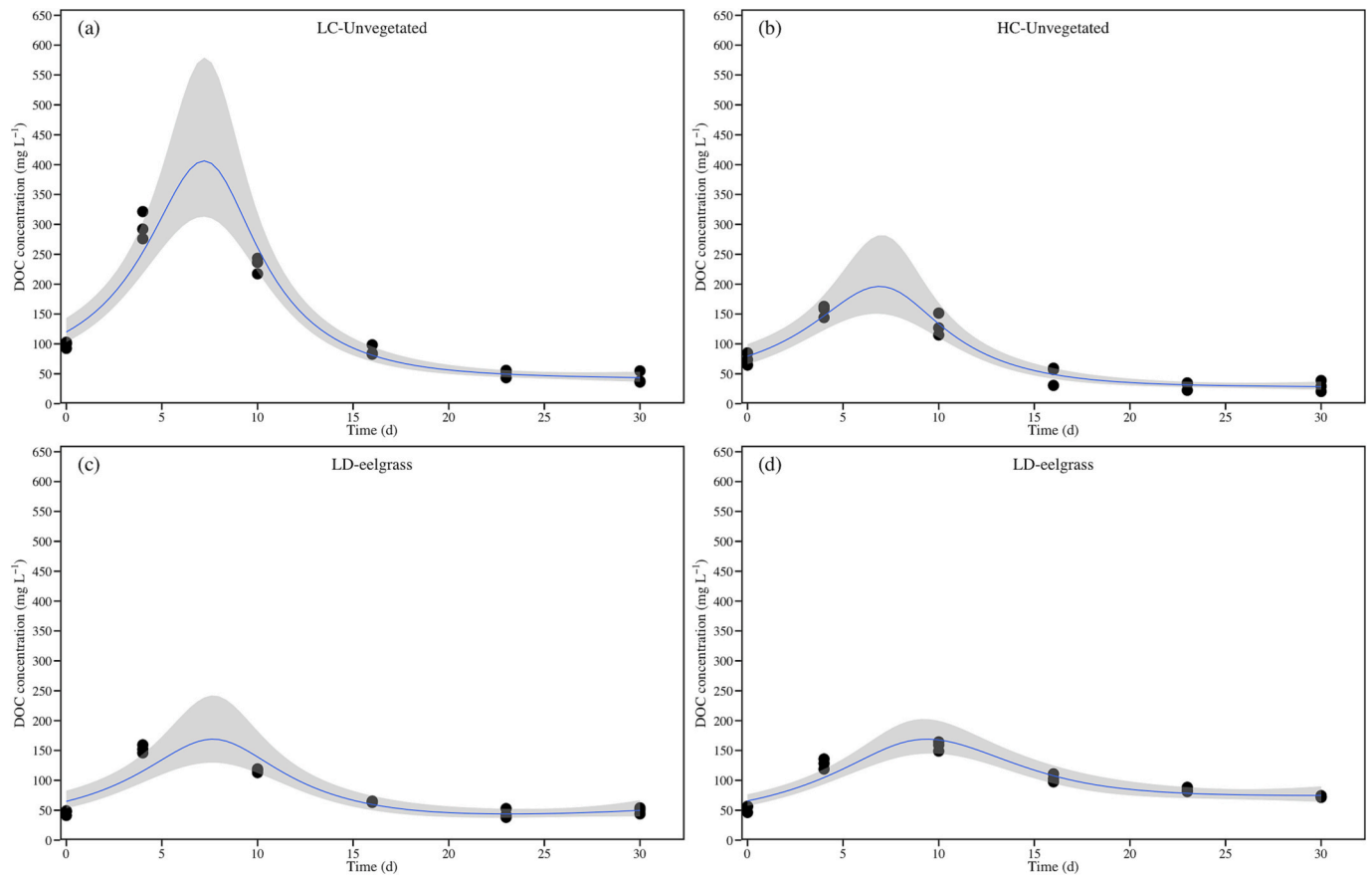


Fig. 6. Assessment of DOC bioavailability in unvegetated and eelgrass sediments. LC- and HC-unvegetated: lower- and higher-carbon concentration unvegetated sediment, LD- and HD-eelgrass: lower- and higher-density eelgrass. Points represent the mean ($n = 3$) of DOC concentration through the time. Lines show the GAM regressions fitted to each plot, with shaded areas representing the 95 % GAM confidence intervals.

vulnerable to remineralization. The OC stored in meadows formed by larger and more persistent seagrass species will likely exhibit a lower OC decay rates, as noted in previous works (Mazarrasa et al., 2018). In addition, the results show here derived from the top 1 cm of sediment layer, which is mainly formed by recently deposited organic detritus with higher oxic conditions. Nonetheless, a relatively high amount of OC remained after 30 day of high remineralization condition exposure in sediments from HD-eelgrass samples ($118 \pm 22 \text{ g m}^{-2}$ sediment surface; 1 cm depth) similar to OC stocks recorder in eelgrass meadows from Finland and Denmark (ranged $627\text{--}4324 \text{ g C m}^{-2}$ sediment surface; 25 cm depth; Röhr et al., 2016) demonstrating the potential of eelgrass from Baltic Sea on the formation of blue carbon deposits. The analysis of isotope signal of this remained OC showed a move of $\delta^{13}\text{C}$ toward isotopic signal of seagrass leaves evidencing that the most of refractory carbon had a high contribution of autochthonous seagrass tissues (Fig. S3). However, further research evaluating the contribution of terrestrial source as refractory C to coastal seagrass communities may be considered to integrate totally OM sources.

Along the first period of remineralization assay (i.e., until 10th day), DOC concentration increased substantially in all sediments, as a consequence of POC leaching as DOC (Fig. 4). After those increases, DOC concentration showed a marked decrease, denoting a high lability of leached DOC. According to previous works (Maher and Eyre, 2010), the lowest leached DOC consumption was observed in HD-eelgrass meadow, implying a higher fraction of recalcitrant DOC (up to $72.6 \pm 0.9 \text{ mg DOC L}^{-1}$) which match with the relatively more refractory nature of seagrass detritus (Trevathan-Tackett et al., 2017). Although this amount of recalcitrant DOC can be considered as minor importance for C sequestration, it is important to highlight that the results reported here are

limited this top 1 cm of sediment where, as noted previously, the OC stocks are mainly labile. Deeper sediment layers (>10 cm depth) in vegetated coastal areas usually show higher DOC concentration (up to one magnitude order higher) than the top 1–2 cm of sediment layer (Chipman et al., 2012) and the decay of OC from those deeper sediment layers may result in higher recalcitrant DOC release. The potential of remineralization of OC stocks in deeper sediments layer of seagrass meadows should be further explored in future researches in order to predict the fate of the carbon stored in these ecosystems when meadow is degraded or loss.

5. Conclusions

Our results showed that the presence of seagrass reduced sediment erosion and OC loss, but only in the case of high-density canopies. However, a decrease in seagrass density could promote the resuspension of sedimentary OC. Both unidirectional and oscillatory flows released similar amounts of DOC from surface sediments, while oscillatory flow released significantly more POC compared to unidirectional flows. A positive correlation between DOC and POC was found in this study, suggesting that POC can leach into DOC, with the DOC being predominantly labile. Additionally, all sediment types exhibited a high rates of OC decay (>74 % within 30 days). Although the most of OC was remineralized as CO₂ under long remineralization condition exposure, a relatively high amount of OC remained in sediments with higher eelgrass canopy density, indicating the potential for the formation of ocean blue carbon deposits. This study revealed the vulnerability of the large OC deposits in seagrass sediments to erosion and resuspension under future environmental conditions characterized by higher storm

frequency and intensity. This loss of both particulate and dissolved organic carbon from the upper sediment layer, which otherwise could have contributed to the sedimentary carbon stock, may weaken the seagrass meadows' ability to sequester carbon in the future.

CRedit authorship contribution statement

L.G. Egea: Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Funding acquisition. **E. Infantes:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Funding acquisition. **R. Jiménez-Ramos:** Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.165976>.

References

- Adhitya, A., Bouma, T., Folkard, A., van Katwijk, M., Callaghan, D., de Iongh, H., Herman, P., 2014. Comparison of the influence of patch-scale and meadow-scale characteristics on flow within seagrass meadows: a flume study. *Mar. Ecol. Prog. Ser.* 516, 49–59. <https://doi.org/10.3354/meps10873>.
- Adhitya, A., Folkard, A.M., Govers, L.L., van Katwijk, M.M., de Iongh, H.H., Herman, P. M.J., Bouma, T.J., 2016. The exchange of dissolved nutrients between the water column and substrate pore-water due to hydrodynamic adjustment at seagrass meadow edges: a flume study. *Limnol. Oceanogr.* 61, 2286–2295. <https://doi.org/10.1002/lno.10376>.
- Atwood, T.B., Witt, A., Mayorga, J., Hammill, E., Sala, E., 2020. Global patterns in marine sediment carbon stocks. *Front. Mar. Sci.* 7, 165. <https://doi.org/10.3389/fmars.2020.00165>.
- Barcelona, A., Oldham, C., Colomer, J., Garcia-Orellana, J., Serra, T., 2021. Particle capture by seagrass canopies under an oscillatory flow. *Coast. Eng.* 169, 103972. <https://doi.org/10.1016/j.coastaleng.2021.103972>.
- Bouma, T., Friedrichs, M., Klaassen, P., van Wesenbeeck, B., Brun, F., Temmerman, S., van Katwijk, M., Graf, G., Herman, P., 2009. Effects of shoot stiffness, shoot size and current velocity on scouring sediment from around seedlings and propagules. *Mar. Ecol. Prog. Ser.* 388, 293–297. <https://doi.org/10.3354/meps08130>.
- Burdige, D.J., Alperin, M.J., Homstead, J., Martens, C.S., 1992. The role of benthic fluxes of dissolved organic carbon in oceanic and sedimentary carbon cycling. *Geophys. Res. Lett.* 19, 1851–1854. <https://doi.org/10.1029/92GL02159>.
- Castaldelli, G., Welsh, D.T., Flachi, G., Zucchini, G., Colombo, G., Rossi, R., Fano, E.A., 2003. Decomposition dynamics of the bloom forming macroalga *Ulva rigida* C. Agardh determined using a ¹⁴C-carbon radio-tracer technique. *Aquat. Bot.* 75, 111–122. [https://doi.org/10.1016/S0304-3770\(02\)00167-5](https://doi.org/10.1016/S0304-3770(02)00167-5).
- Chen, Z., Nie, T., Zhao, X., Li, J., Yang, B., Cui, D., Li, X., 2022. Organic carbon remineralization rate in global marine sediments: a review. *Reg. Stud. Mar. Sci.* 49, 102112. <https://doi.org/10.1016/j.rsma.2021.102112>.
- Chipman, L., Huettel, M., Laschet, M., 2012. Effect of benthic-pelagic coupling on dissolved organic carbon concentrations in permeable sediments and water column in the northeastern Gulf of Mexico. *Cont. Shelf Res.* 45, 116–125. <https://doi.org/10.1016/j.csr.2012.06.010>.
- Dahl, M., Infantes, E., Clevesjö, R., Linderholm, H.W., Björk, M., Gullström, M., 2018. Increased current flow enhances the risk of organic carbon loss from *Zostera marina* sediments: insights from a flume experiment. *Limnol. Oceanogr.* 63, 2793–2805. <https://doi.org/10.1002/lno.11009>.
- Dahl, M., Asplund, M.E., Björk, M., Deyanova, D., Infantes, E., Isaeus, M., Nyström Sandman, A., Gullström, M., 2020. The influence of hydrodynamic exposure on carbon storage and nutrient retention in eelgrass (*Zostera marina* L.) meadows on the Swedish Skagerrak coast. *Sci. Rep.* 10, 13666. <https://doi.org/10.1038/s41598-020-70403-5>.
- Duarte, C.M., Krause-Jensen, D., 2017. Export from seagrass meadows contributes to marine carbon sequestration. *Front. Mar. Sci.* 4, 13. <https://doi.org/10.3389/fmars.2017.00013>.
- Duarte, C.M., Holmer, M., Marbà, N., 2005. Plant-microbe interactions in seagrass meadows. In: Kristensen, E., Haese, R.R., Kostka, J.E. (Eds.), *Interactions Between Macro- and Microorganisms in Marine Sediments*. American Geophysical Union, Washington, pp. 31–60. <https://doi.org/10.1029/CE060p0031>.
- Duarte, C.M., Losada, I.J., Hendriks, I.E., Mazarrasa, I., Marbà, N., 2013. The role of coastal plant communities for climate change mitigation and adaptation. *Nat. Clim. Chang.* 3, 961–968. <https://doi.org/10.1038/nclimate1970>.
- Dunic, J.C., Brown, C.J., Connolly, R.M., Turschwell, M.P., Côté, I.M., 2021. Long-term declines and recovery of meadow area across the world's seagrass bioregions. *Glob. Chang. Biol.* 27, 4096–4109. <https://doi.org/10.1111/gcb.15684>.
- Egea, L.G., Jiménez-Ramos, R., Hernández, I., Bouma, T.J., Brun, F.G., 2018. Effects of ocean acidification and hydrodynamic conditions on carbon metabolism and dissolved organic carbon (DOC) fluxes in seagrass populations. *PLoS One* 13, e0192402. <https://doi.org/10.1371/journal.pone.0192402>.
- Egea, L.G., Barrón, C., Jiménez-Ramos, R., Hernández, I., Vergara, J.J., Pérez-Lloréns, J. L., Brun, F.G., 2019. Coupling carbon metabolism and dissolved organic carbon fluxes in benthic and pelagic coastal communities. *Estuar. Coast. Shelf Sci.* 227, 106336. <https://doi.org/10.1016/j.ecss.2019.106336>.
- Egea, L.G., Jiménez-Ramos, R., Romera-Porras, I., Bonet-Melià, P., Yamaza-Magdalena, A., Cerezo-Sepúlveda, L., Pérez-Lloréns, J.L., Brun, F.G., 2023. Effect of marine heat waves on carbon metabolism, optical characterization, and bioavailability of dissolved organic carbon in coastal vegetated communities. *Limnol. Oceanogr.* 68, 467–482. <https://doi.org/10.1002/lno.12286>.
- Fonseca, M.S., Fourqurean, J.W., Koehl, M.A.R., 2019. Effect of seagrass on current speed: importance of flexibility vs. shoot density. *Front. Mar. Sci.* 6, 376. <https://doi.org/10.3389/fmars.2019.00376>.
- Gasol, J.M., Del Giorgio, P.A., 2000. Using flow cytometry for counting natural planktonic bacteria and understanding the structure of planktonic bacterial communities. *Sci. Mar.* 64, 197–224. <https://doi.org/10.3989/scimar.2000.64n2197>.
- Hansell, D.A., 2013. Recalcitrant dissolved organic carbon fractions. *Annu. Rev. Mar. Sci.* 5, 421–445. <https://doi.org/10.1146/annurev-marine-120710-100757>.
- Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E. D., Robinson, B.S., Hodgson, D.J., Inger, R., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6, e4794. <https://doi.org/10.7717/peerj.4794>.
- Hilmi, N., Chami, R., Sutherland, M.D., Hall-Spencer, J.M., Lebleu, L., Benitez, M.B., Levin, L.A., 2021. The role of blue carbon in climate change mitigation and carbon stock conservation. *Front. Clim.* 3, 710546. <https://doi.org/10.3389/fclim.2021.710546>.
- Hoikkala, L., Lahtinen, T., Pertilä, M., Lignell, R., 2012. Seasonal dynamics of dissolved organic matter on a coastal salinity gradient in the northern Baltic Sea. *Cont. Shelf Res.* 45, 1–14. <https://doi.org/10.1016/j.csr.2012.04.008>.
- Coastal blue carbon: methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrass meadows.** In: Howard, J., Hoyt, S., Isensee, K., Pidgeon, E., Telszewski, M. (Eds.), 2014. *Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature*. Arlington, Virginia, USA.
- Infantes, E., Orfila, A., Simarro, G., Luhar, M., Terrados, J., Nepf, H., 2012. Effect of a seagrass (*Posidonia oceanica*) meadow on wave propagation. *Mar. Ecol. Prog. Ser.* 456, 63–72. <https://doi.org/10.3354/meps09754>.
- Infantes, E., Smit, J.C., Tamarit, E., Bouma, T.J., 2021. Making realistic wave climates in low-cost wave mesocosms: a new tool for experimental ecology and biogeomorphology. *Limnol. Oceanogr. Methods* 19, 317–330. <https://doi.org/10.1002/lom3.10425>.
- Infantes, E., Hoeks, S., Adams, M., van der Heide, T., van Katwijk, M., Bouma, T., 2022. Seagrass roots strongly reduce cliff erosion rates in sandy sediments. *Mar. Ecol. Prog. Ser.* 700, 1–12. <https://doi.org/10.3354/meps14196>.
- Jacobs, W., Le Hir, P., Van Kesteren, W., Cann, P., 2011. Erosion threshold of sand–mud mixtures. *Cont. Shelf Res.* 31, S14–S25. <https://doi.org/10.1016/j.csr.2010.05.012>.

- Jiao, N., Herndl, G.J., Hansell, D.A., Benner, R., Kattner, G., Wilhelm, S.W., Kirchman, D.L., Weinbauer, M.G., et al., 2010. Microbial production of recalcitrant dissolved organic matter: long-term carbon storage in the global ocean. *Nat. Rev. Microbiol.* 8, 593–599. <https://doi.org/10.1038/nrmicro2386>.
- Jiménez-Ramos, R., Tomas, F., Reynés, X., Romera-Castillo, C., Pérez-Lloréns, J.L., Egea, L.G., 2022. Carbon metabolism and bioavailability of dissolved organic carbon (DOC) fluxes in seagrass communities are altered under the presence of the tropical invasive alga *Halimeda incrassata*. *Sci. Total Environ.* 839, 156325 <https://doi.org/10.1016/j.scitotenv.2022.156325>.
- Jiménez-Ramos, R., Brun, F.G., Pérez-Lloréns, J.L., Vergara, J.J., Delgado-Cabezas, F., Sena-Soria, N., Egea, L.G., 2023. Resistance and recovery of benthic marine macrophyte communities to light reduction: insights from carbon metabolism and dissolved organic carbon (DOC) fluxes, and implications for resilience. *Mar. Pollut. Bull.* 188, 114630 <https://doi.org/10.1016/j.marpolbul.2023.114630>.
- Kennedy, P., Kennedy, H., Papadimitriou, S., 2005. The effect of acidification on the determination of organic carbon, total nitrogen and their stable isotopic composition in algae and marine sediment. *Rapid Commun. Mass Spectrom.* 19, 1063–1068. <https://doi.org/10.1002/rcm.1889>.
- Lavery, P.S., Oldham, C.E., Ghisalberti, M., 2001. The use of Fick's First Law for predicting porewater nutrient fluxes under diffusive conditions. *Hydrol. Process.* 15, 2435–2451. <https://doi.org/10.1002/hyp.297>.
- Lavery, P.S., McMahon, K., Weyers, J., Boyce, M.C., Oldham, C.E., 2013. Release of dissolved organic carbon from seagrass wrack and its implications for trophic connectivity. *Mar. Ecol. Prog. Ser.* 494, 121–133. <https://doi.org/10.3354/meps10554>.
- Lenth, R., Singmann, H., Love, J., Buerkner, P., Herve, M., 2019. *Emmeans: Estimated Marginal Means, aka Least-squares Means. R Package, Version 1.3.3*.
- Liu, S., Jiang, Z., Zhou, C., Wu, Y., Arbi, I., Zhang, J., Huang, X., Trevathan-Tackett, S.M., 2018. Leaching of dissolved organic matter from seagrass leaf litter and its biogeochemical implications. *Acta Oceanol. Sin.* 37, 84–90. <https://doi.org/10.1007/s13131-018-1233-1>.
- Maciejewska, A., Pempkowiak, J., 2014. DOC and POC in the water column of the southern Baltic. Part I. evaluation of factors influencing sources, distribution and concentration dynamics of organic matter. *Oceanologia* 56, 523–548. <https://doi.org/10.5697/oc.55-3.523>.
- Macreadie, P.I., Baird, M.E., Trevathan-Tackett, S.M., Larkum, A.W.D., Ralph, P.J., 2014. Quantifying and modelling the carbon sequestration capacity of seagrass meadows – a critical assessment. *Mar. Pollut. Bull.* 83, 430–439. <https://doi.org/10.1016/j.marpolbul.2013.07.038>.
- Maher, D.T., Eyre, B.D., 2010. Benthic fluxes of dissolved organic carbon in three temperate Australian estuaries: implications for global estimates of benthic DOC fluxes. *J. Geophys. Res.* 115, G04039. <https://doi.org/10.1029/2010JG001433>.
- Marin-Diaz, B., Bouma, T.J., Infantes, E., 2020. Role of eelgrass on bed-load transport and sediment resuspension under oscillatory flow. *Limnol. Oceanogr.* 65, 426–436. <https://doi.org/10.1002/lno.11312>.
- Massana, R., Pedrós-Alió, C., Casamayor, E.O., Gasol, J.M., 2001. Changes in marine bacterioplankton phylogenetic composition during incubations designed to measure biogeochemically significant parameters. *Limnol. Oceanogr.* 46, 1181–1188. <https://doi.org/10.4319/lo.2001.46.5.1181>.
- Mazarrasa, I., Samper-Villarreal, J., Serrano, O., Lavery, P.S., Lovelock, C.E., Marbà, N., Duarte, C.M., Cortés, J., 2018. Habitat characteristics provide insights of carbon storage in seagrass meadows. *Mar. Pollut. Bull.* 134, 106–117. <https://doi.org/10.1016/j.marpolbul.2018.01.059>.
- McLeod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B.R., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Front. Ecol. Environ.* 9, 552–560. <https://doi.org/10.1890/110004>.
- Moksnes, P., Röhr, M.E., Holmer, M., Eklöf, J.S., Eriander, L., Infantes, E., Boström, C., 2021. Major impacts and societal costs of seagrass loss on sediment carbon and nitrogen stocks. *Ecosphere* 12 (7), e03658. <https://doi.org/10.1002/ecs2.3658>.
- Navarro, N., Agustí, S., Duarte, C.M., 2004. Plankton metabolism and DOC use in the Bay of Palma, NW Mediterranean Sea. *Aquat. Microb. Ecol.* 37, 1–24. <https://doi.org/10.3354/ame037047>.
- Oguz, E., Elginöz, N., Koroglu, A., Kabdasli, M.S., 2013. The effect of reed beds on wave attenuation and suspended sediment concentration. *J. Coast. Res.* 65, 356–361. <https://doi.org/10.2112/SI65-061.1>.
- Parnell, A.C., 2019. Package “simmr”: A Stable Isotope Mixing Model. [R Programming Language].
- Pendleton, L., Donato, D.C., Murray, B.C., Crooks, S., Jenkins, W.A., Sifleet, S., Craft, C., Fourqurean, J.W., et al., 2012. Estimating global “blue carbon” emissions from conversion and degradation of vegetated coastal ecosystems. *PLoS One* 7, e43542. <https://doi.org/10.1371/journal.pone.0043542>.
- Pereda-Briones, L., Infantes, E., Orfila, A., Tomas, F., Terrados, J., 2018. Dispersal of seagrass propagules: interaction between hydrodynamics and substratum type. *Mar. Ecol. Prog. Ser.* 593, 47–59. <https://doi.org/10.3354/meps12518>.
- Pineiro-Juncal, N., Kaal, J., Moreira, J.C.F., Martínez Cortizas, A., Lambais, M.R., Otero, X.L., Mateo, M.A., 2021. Cover loss in a seagrass *Posidonia oceanica* meadow accelerates soil organic matter turnover and alters soil prokaryotic communities. *Org. Geochem.* 151, 104140. <https://doi.org/10.1016/j.orggeochem.2020.104140>.
- Potouroglou, M., Bull, J.C., Krauss, K.W., Kennedy, H.A., Fusi, M., Daffonchio, D., Mangora, M.M., Githaiga, M.N., et al., 2017. Measuring the role of seagrasses in regulating sediment surface elevation. *Sci. Rep.* 7, 11917. <https://doi.org/10.1038/s41598-017-12354-y>.
- Röhr, M.E., Boström, C., Canal-Vergés, P., Holmer, M., 2016. Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows. *Biogeosciences* 13, 6139–6153. <https://doi.org/10.5194/bg-13-6139-2016>.
- Ros, A., Colomer, J., Serra, T., Pujol, D., Soler, M., Casamitjana, X., 2014. Experimental observations on sediment resuspension within submerged model canopies under oscillatory flow. *Cont. Shelf Res.* 91, 220–231. <https://doi.org/10.1016/j.csr.2014.10.004>.
- Rühl, S., Thompson, C.E.L., Queirós, A.M., Widdicombe, S., 2020. Intra-annual patterns in the benthic-pelagic fluxes of dissolved and particulate matter. *Front. Mar. Sci.* 7, 567193. <https://doi.org/10.3389/fmars.2020.567193>.
- Schaefer, R.B., Nepf, H.M., 2022. Flow structure in an artificial seagrass meadow in combined wave-current conditions. *Front. Mar. Sci.* 9. <https://doi.org/10.3389/fmars.2022.836901>.
- Sitterley, K.A., Silverstein, J., Rosenblum, J., Linden, K.G., 2021. Aerobic biological degradation of organic matter and fracturing fluid additives in high salinity hydraulic fracturing wastewaters. *Sci. Total Environ.* 758, 143622. <https://doi.org/10.1016/j.scitotenv.2020.143622>.
- Trevathan-Tackett, S., Macreadie, P., Sanderman, J., Baldock, J., Howes, J., Ralph, P., 2017. A global assessment of the chemical recalcitrance of seagrass tissues: implications for long-term carbon sequestration. *Front. Plant Sci.* 8, 925. <https://doi.org/10.3389/fpls.2017.00925>.
- Trevathan-Tackett, S.M., Jeffries, T.C., Macreadie, P.I., Manojlovic, B., Ralph, P., 2020. Long-term decomposition captures key steps in microbial breakdown of seagrass litter. *Sci. Total Environ.* 705, 135806. <https://doi.org/10.1016/j.scitotenv.2019.135806>.
- Vanholme, R., Demedts, B., Morreel, K., Ralph, J., Boerjan, W., 2010. Lignin biosynthesis and structure. *Plant Physiol.* 153, 895–905. <https://doi.org/10.1104/pp.110.155119>.
- Vichkovitten, T., Holmer, M., 2005. Dissolved and particulate organic matter in contrasting *Zostera marina* (eelgrass) sediments. *J. Exp. Mar. Biol. Ecol.* 316, 183–201. <https://doi.org/10.1016/j.jembe.2004.11.002>.
- Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. *J. Geol.* 30, 377–392.
- Wesslander, K., Viktorsson, L., Skjevik, A.-T., 2018. *The Swedish National Marine Monitoring Programme. Report Oceanography No. 64, p. 122*.
- Wood, S.N., 2017. *Generalized Additive Models. Chapman and Hall/CRC*. <https://doi.org/10.1201/9781315370279>.
- Zhang, J., Lei, J., Huai, W., Nepf, H., 2020. Turbulence and particle deposition under steady flow along a submerged seagrass meadow. *J. Geophys. Res. Ocean.* 125. <https://doi.org/10.1029/2019JC015985>.