Estuarine, Coastal and Shelf Science 272 (2022) 107896

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Vertical intertidal variation of organic matter stocks and patterns of sediment deposition in a mesotidal coastal wetland

Carmen B. de los Santos [a,*], François Lahuna [b], André Silva [a], Cátia Freitas [a,c], Márcio Martins [a], A. Rita Carrasco [d], Rui Santos [a]

[a] Centre of Marine Sciences of Algarve (CCMAR), University of Algarve, Gambelas Campus, Faro, 8005-139, Portugal
[b] University Pierre et Marie Curie, 75005, Paris, France
[c] School of Life and Environmental Sciences, Deakin University, Waurn Ponds Campus, Geelong, Australia
[d] Centre for Marine and Environmental Research (CIMA), University of Algarve, Gambelas Campus, Faro, 8005-139, Portugal

ARTICLE INFO

Keywords:
Organic matter
Sediment deposition
Hydroperiod
Tidal wetland
Seagrass
Salt marsh

ABSTRACT

Tidal coastal wetlands, common home to seagrass and salt marshes, are relevant carbon sinks due to their high capacity to accumulate and store organic carbon in their sediments. Recent studies demonstrated that the spatial variability of this organic carbon within the same wetland system can be significant. Some of the environmental drivers of this spatial variability remain understudied and the selection of the most relevant ones can be context dependent. Here we investigated the role of bed elevation, hydrodynamics, and habitat type (salt marsh and seagrass) on the organic matter (OM) net deposition-resuspension rate and superficial sedimentary stocks (top 5 cm) at the tidal wetlands of the Ria Formosa, a mesotidal coastal lagoon in South Portugal. Results showed that two vectors of spatial variation need to be considered to describe the intertidal sedimentary OM stocks: the bed elevation that imposes a decrease of the hydroperiod and thus the change of habitat from the lower seagrass *Z. noltei* to the upper saltmarsh *S. maritimus*, and the horizontal spatial variation along the secondary channels of the lagoon that imposes a decrease in the current flow velocity magnitude. The multiple linear regression analyses, using data from 40 sampling points, explained 59% of the variation of the superficial sedimentary stocks of OM in salt marshes and seagrasses of the Ria Formosa lagoon and revealed that stocks generally decrease with elevation, yet with variation among sites and habitats. It was also found that the decrease of the OM net deposition-resuspension rate with bed elevation was exponential. Our study emphasizes the importance of considering multiple environmental drivers and spatial variation for regional estimations of organic matter (and organic carbon) sedimentary stocks in coastal wetlands.

1. Introduction

Tidal coastal wetlands in temperate regions are commonly home to seagrass meadows and salt marshes. These coastal vegetated habitats, along with mangroves, rank amongst the most efficient carbon dioxide (CO_2) sinks, for sequestering it in the form of organic carbon (also called blue carbon), both in their biomass and especially in their sediments (Nellemann et al., 2009). After severe declines in the past decades (Deegan et al., 2012; de los Santos et al., 2019; Dunic et al., 2021), these blue carbon ecosystems are on the focus of conservation and restoration strategies to mitigate climate change under the United Nations Framework Convention on Climate Change (UNFCCC; IPCC, 2019). Indeed, wetlands were added to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories (IPCC et al., 2014), which guides the Paris Agreement Parties to report national inventories of the magnitude and distribution of CO_2 sinks. Yet, there are challenges that need to be addressed to deliver accurate blue carbon inventories (Macreadie et al., 2019). One of them is accounting for the spatial variability in sedimentary organic carbon stocks at the wetland level. To do so, the drivers of the spatial variability must be identified and used as predictors in blue carbon assessments with the final aim of reducing estimation errors.

The spatial variation in the sedimentary organic carbon stocks in seagrass and salt marshes can be controlled by a variety of biophysical drivers at the regional level (Ouyang and Lee, 2014; Mazarrasa et al., 2018; Ewers Lewis et al., 2020; Ricart et al., 2020; Novak et al., 2020). When these ecosystems are present in tide-controlled systems, common

* Corresponding author.
E-mail address: cbsantos@ualg.pt (C.B. de los Santos).

https://doi.org/10.1016/j.ecss.2022.107896
Received 27 August 2021; Received in revised form 26 January 2022; Accepted 9 May 2022
Available online 13 May 2022

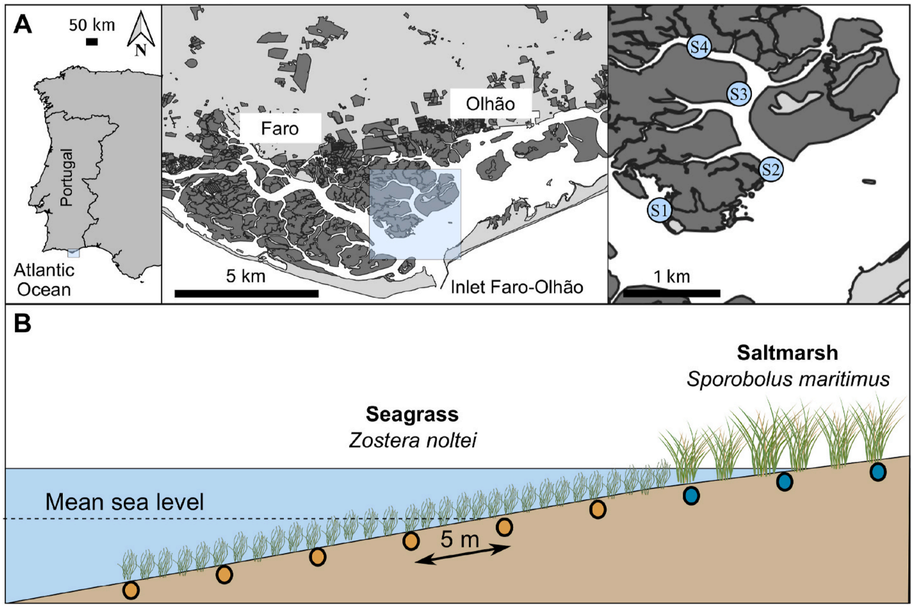

Fig. 1. (A) Location of the Ria Formosa lagoon (South Portugal) showing the sampling sites along the gradient of current flow velocity, from the most exposed station (S1) to the most sheltered one (S4), and (B) scheme of the transects in the intertidal area showing the sampling points separated every 5 m at *Zostera noltei* seagrass beds (brown circles) and *Sporobolus maritimus* saltmarsh patches (blue circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

drivers are vegetation habitat composition, hydrodynamics, tidal range, and bed elevation (Ouyang and Lee, 2014; Kelleway et al., 2017; Zhang et al., 2017; Santos et al., 2019; Jiménez-Arias et al., 2020; Lima et al., 2020; Martins et al., 2021). These environmental drivers can be significant when comparing different wetlands (e.g., wetlands subjected to different tidal regimes), but also within the same system if they vary substantially in space. Thus, it would be desirable to identify those drivers at the local or regional scale, where comprehensive blue carbon maps are to be obtained (Ewers Lewis et al., 2020). Looking for easy-to-measure blue carbon predictors at local or regional scales would facilitate the creation of accurate maps of blue carbon stocks in coastal tidal wetlands (Ford et al., 2019). The first step would then consist of investigating the existence of strong relationships between biophysical factors and sedimentary organic carbon stocks.

The sedimentary organic carbon stock is a balance of inputs and outputs of organic matter (OM) in the sediment compartment. Many processes are involved in this balance, such as OM deposition, retention, exportation, preservation and remineralization (Mateo et al., 2006). In the top sediment layer, where most of the organic carbon is stored, one of the first processes to control the OM input is the deposition of suspended particulate organic matter from the water column into the sediment. Sedimentation patterns in tidal marshes can be controlled by a series of biophysical factors with a high spatial variability, both horizontally and vertically (e.g., Cahoon and Reed, 1995; French et al., 1995; Leonard, 1997; Butzeck et al., 2015; Kelleway et al., 2017). The intensity of the horizontal flow velocity, the turbulent energy of the flow, and the particle settling velocity determines if the sediment is transported or if it settles down (Christiansen et al., 2000 and references therein), influencing the organic carbon stock and sequestration rate in intertidal areas (Santos et al., 2019; Martins et al., 2021). The tidal marsh vegetation can also influence the settling of the suspended particles and prevent further sediment resuspension of the particles trapped (Leonard and Luther, 1995; Leonard et al., 1997; Nepf et al., 1997; Christiansen et al., 2000; Kelleway et al., 2017). Bed elevation also strongly affects the sedimentation pattern in intertidal areas, with higher rates at the low elevation zone (Chmura et al., 2003; Neumeier and Ciavola, 2004), through the control of the water depth and the inundation time and frequency (Bockelmann et al., 2002). Bed elevation can also determine the habitat type, since the occurring of plant communities along the vertical zonation depends on the tidal flooding regime through their limits in inundation and salinity tolerance (Pennings and Callaway, 1992; Hansen et al., 2017). Indeed, bed elevation has been identified as a relevant driver in explaining the spatial vertical variability in sedimentary carbon stocks (Chmura et al., 2003; Hansen et al., 2017). In summary, bed elevation integrates multiple biophysical factors potentially affecting the vertical spatial pattern of sedimentary carbon stocks in tidal wetlands. Together with current flow velocity, which can have large variations across space in shallow semi-enclosed wetlands (Carrasco et al., 2018), bed elevation may explain the spatial variability of blue carbon stocks in coastal wetlands. Since the spatial variability of current flow velocity and bed elevation can be obtained from regional hydrodynamics models (Möller and Christie, 2019) and high-resolution digital elevation models (DEM) generated by airborne and stationary Lidar (Pham et al., 2019), respectively, they are promising candidates for modelling blue carbon stocks in tidal wetlands.

The aim of this work is to address how the biophysical drivers bed elevation, vegetated habitat type, and flow velocity determine blue carbon stocks in mesotidal coastal wetlands. Specifically, we aimed at providing an empirical function model to estimate the OM superficial sedimentary stocks, as a proxy for blue carbon stocks, in Ria Formosa lagoon (South Portugal) based on those drivers. We hypothesise that organic matter stocks will vary spatially at two dimensions: horizontally along a flow velocity gradient (as previously shown by Santos et al., 2019, Martins et al., 2021), with larger stocks at low flow velocity sites, and vertically, with bed elevation, hydroperiod, and vegetation composition, expecting the lower the bed elevation, the larger the stocks within the same vegetation type. The OM stocks were quantified along the vertical distribution of the two co-occurring intertidal vegetated habitats, the lower intertidal seagrass *Zostera noltei* and upper saltmarsh *Sporobolus maritimus*, in sites along a horizontal current flow velocity gradient. To understand the processes behind OM stock observations, the OM contents of the recent deposited-resuspended sediment and its net deposition-resuspension rate were also investigated.

2. Materials and methods

2.1. Study site and sampling design

Ria Formosa is a sheltered mesotidal lagoon in southern Portugal resulting from a barrier-island system connected to the Atlantic Ocean through six inlets (Fig. 1A). The lagoon has a triangular shape, about 55

Table 1
Characterisation of the transects laid along the vertical slope from seagrass meadows of *Zostera noltei* (Zn) to salt marsh patches of *Sporobolus maritimus* (Sm) at the four sampling sites, from the highest (S1) to the lowest (S4) current flow velocity. Bed elevation range (minimum and maximum) is referred to mean sea level (MSL). Hydroperiod range is expressed as the percentage of submersion time during March 2017, and the range of the water column heights refers to values estimated for the same month.

Site	Habitat	Sampling points	Slope (%)	Minimum elevation (m, MSL)	Maximum elevation (m, MSL)	Hydroperiod (%)	Water column height (m)	Canopy height (cm)
S1	Zn	5	0.6	0.30	0.39	36–40	0.0–1.4	12.5 ± 1.3
	Sm	2	1.1	0.63	0.87	18–27	0.0–1.1	18.3 ± 3.9
S2	Zn	6	6.2	−0.80	0.22	42–79	0.0–2.5	4.5 ± 0.7
	Sm	3	1.0	0.41	0.65	26–35	0.0–1.3	13.9 ± 0.7
S3	Zn	13	2.8	−1.44	0.16	44–96	0.0–3.1	11.7 ± 1.1
	Sm	5	0.1	0.24	0.36	37–42	0.0–1.5	29.0 ± 2.0
S4	Zn	3	11.4	−0.49	0.07	47–67	0.0–2.2	5.9 ± 0.7
	Sm	3	5.0	0.11	0.60	28–46	0.0–1.6	32.8 ± 2.4

km long (E-W) and 6 km wide (N–S) at its widest zone, covering a wet surface area of 105 km^2 with a mean depth of 3 m. Tides are semi-diurnal with amplitudes ranging from 1.5 m in neap tides to 3.5 m in spring tides, which makes two thirds of the lagoon intertidal during an average low tide (Dias et al., 2009). The Ria Formosa is characterized by a network of numerous channels and extensive tidal flats which are intersected by a high density of shallow meandering tidal creeks. The back-barrier intertidal mudflats are largely colonised by monospecific meadows of seagrass species *Zostera noltei* and saltmarsh species *Sporobolus maritimus* (Fig. 1B), the latter being intersected by a high density of shallow meandering tidal creeks. *Zostera noltei* occupies a vertical gradient of about 2 m (Silva and Santos, 2003). Its upper limit coincides with the lower limit of *S. maritimus* and the lower limit with the transition to the subtidal area, commonly dominated by seagrass species *Cymodocea nodosa* and, to a lower extent, *Z. marina*. The system receives little freshwater inputs from rivers (Malta et al., 2017) and water circulation is mostly driven by tides (Jacob et al., 2013).

Four sampling sites (S1 to S4, Fig. 1B) were selected along a well-studied gradient of flow current velocity, a key factor determining sedimentary organic matter and organic carbon stocks in the Ria Formosa (Santos et al., 2019; Martins et al., 2021). The gradient was characterised by an increase in the relative frequencies of low velocities (0–0.2 m s^{-1}) from S1 to S4, and a decrease in the frequency of high velocities (0.2–0.6 m s^{-1}) from S1 to S4 (Santos et al., 2019), based on a validated process-based model of depth-average current velocities for the Ria Formosa lagoon (Carrasco et al., 2018). This current velocity gradient was reflected in the sediment properties, as mean grain size of sediments decreased from S1 to S4, in both the *S. maritimus* and *Z. noltei* sediments, and clay mineral content increased from S1 to S4 (Santos et al., 2019).

At each site, cross-shore transects were laid to encompass the longest available vegetated length, perpendicular to the shore, from the lower intertidal dominated by the seagrass *Z. noltei* (Zn) to the upper intertidal dominated by the saltmarsh *S. maritimus* (Sm) (Fig. 1B). Within that selected area, the transect crossed the meadows through their central areas, to avoid edge effects. Transect length at each site was: 30 m at S1, 40 m at S2, 85 m at S3, and 15 at S4. Along each transect, the bed elevation profile was measured, the hydroperiod was estimated, and both the superficial sediment and the sediment net deposition-resuspension rates were sampled every 5 m. The four transects included 40 sampling points, 27 in *Z. noltei* and 13 in *S. maritimus* (Table 1, coordinates of sampling points and variables measured at them are given in the Supplementary Material). Canopy height was measured with a rule (±0.1 cm) in five replicates of *Z. noltei* or *S. maritimus* shoots collected next to each sampling point. The field work was conducted during equinoctial spring tides, from the 28^{th} to 31^{st} of March 2017.

2.2. Bed elevation and hydroperiod

Transect profiles were done by measuring the coordinates (UTM, m; ETRS89, Portugal TM06) and the bed elevation (m, referred to mean sea level, MSL) along each transect, sampling at 1 Hz with a Real-Time Kinematic Differential Global Positioning System (RTK-DGPS, Trimble R6). The slope of each habitat within a transect was calculated as the ratio between the vertical distance (rise) and the horizontal distance (run) and expressed in percentage (%). The hydroperiod at each sampling point was estimated as the cumulative submersion time in the month of the sampling period (% of the month). It was used a model based on the official tidal charts (Faro-Olhão, Instituto Hidrográfico de Portugal) that calculates the water depth at 1-m time intervals at a site of known bed elevation. The model was validated against field measurements of water depth at two points along the S3 transect (points 0 and 30 m), measured with a water level logger (Solinst ® Levelogger and In-Situ level troll) at 4 Hz, during two tidal cycles, from 28^{th} to 29^{th} March. Full model explanation, script, data and validation are available at a software repository (de los Santos and Martins, 2021).

2.3. Sediment net deposition-resuspension rate and sedimentary organic matter stock

Sediment traps were installed at each sampling point to measure the sediment net deposition-resuspension rate, which was defined as sediment particles deposited for the first time at the bottom of the measuring site as well as the resuspended material over the time the traps were installed. Traps consisted of 3-cm diameter cylindrical tubes (Falcon® tubes, 11.5 cm long, 50 mL of capacity, opening area of 7.1 cm^2), pre-weighted (±0.01 mg), and labelled. Arrays of paired tubes were evenly attached to a 33-cm long plastic stick, which was buried into the sediment. The openings of the tubes were ~1 cm above the ground to avoid any sediment from saltation to be deposited in the tubes. The OM in the trapped sediment may come from both allochthonous and autochthonous sources, including direct transfer of sediment and OM from the salt marsh to seagrass and vice versa (Santos et al., 2019). The sediment traps were positioned at each sampling point at low spring tide and left in the field for 3 full days (set on March 28^{th}), so that they were collecting particulate matter for 6 tidal cycles. On the retrieval day, during low tide, the traps were carefully capped and replicated superficial sediment samples next to each trap were taken using small corers (diameter 2.5 cm, height 5 cm, n = 3, each sample consisting of two pooled sediment cores). Traps and sediment samples were transported to the laboratory in cool dark conditions and frozen (−20 °C) upon arrival until further processing.

The tubes of the sediment traps were thawed and centrifuged (5 min, 3005 g; HeraeusTM MegafugeTM centrifuge rotor) to decant suspended particles. The supernatant was carefully removed, and the tube content was filtered through a 1-mm mesh sieve (to exclude shell fragments, coarse sediment particles, and plant detrital matter), washed with distilled water (to eliminate salt), centrifuged again (5 min, 3005 g), then oven-dried at 60 °C for 48 h, and weighted (dry weight, dw) in a microbalance (±0.1 mg). The organic matter content (OM, % dw) in the

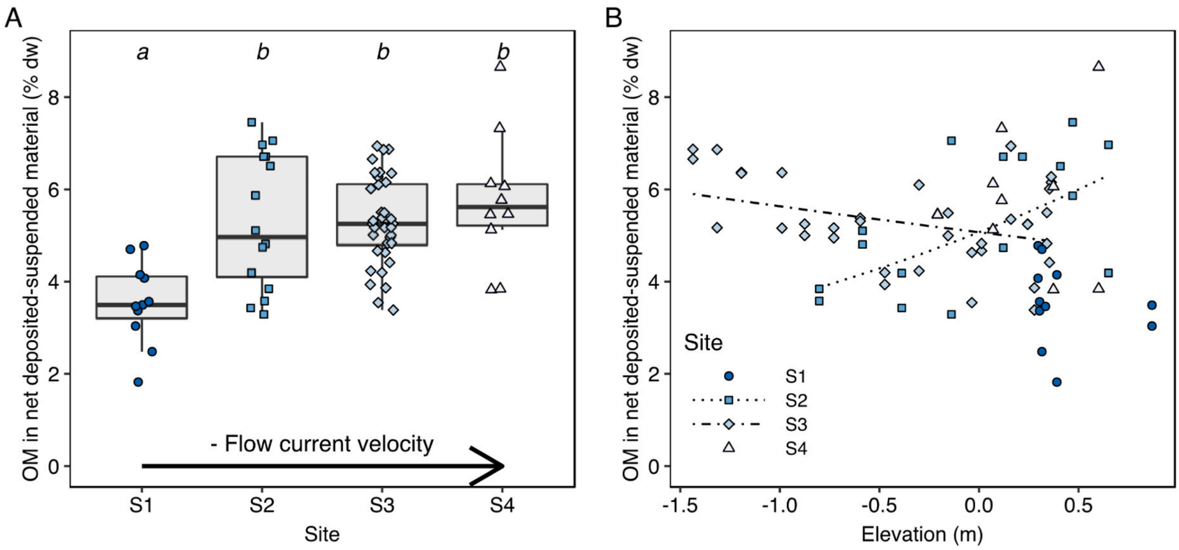

Fig. 2. Significant drivers of variation of the organic matter content (OM, % dw) in the net deposited-suspended material along the vertical intertidal distribution from the lower seagrass *Zostera noltei* to the higher saltmarsh *Sporobolus maritimus* habitats: (A) site, from the highest (S1) to the lowest (S4) current flow velocity; and (B) bed elevation in interaction with site (referred to mean sea level, MSL). Different letters on boxplots in (A) indicate significant differences among sites. Lines in (B) represent the multiple regression models for sites S2 and S3, where the relationship was statistically significant.

trapped sediment was determined by loss on ignition (450 °C, 4 h, Howard et al., 2019) in the two replicates. OM net deposition-resuspension rate (g OM m^{-2} day^{-1}) was calculated for each replicate as the amount of dry sediment times the OM content and per unit of trap surface area and sampling time.

Superficial sediment samples were oven-dried (60 °C, 48 h) and weighted to determine dry bulk density (g dw cm^{-3}), then homogenised with a pestle and a mortar. A subsample of 5 g dw was used to determine the organic matter content (OM, % dw) by loss on ignition (450 °C, 4 h, Howard et al., 2019). Superficial sedimentary stock (g cm^{-2}) of OM at each sampling point was calculated as the dry bulk density times the OM content, times the sampling depth (5 cm). OM stock was used as a proxy of the blue carbon stock through its linear relation with sedimentary organic carbon (OC) content ($OC = -0.3401 + 0.2822 \times OM$, $R^2 = 0.9264$, df = 30, $p < 0.001$; Santos et al., 2019).

2.4. Data analysis

Data are presented as the mean ± SE. Normality (Shapiro-Wilk test) and homoscedasticity (Barlett test) were checked on data, and variables were Ln-transformed when necessary to meet parametric assumptions. Multiple linear regression analyses were used to select which factors best explained the organic matter variables (OM content of the deposited material, OM net deposition-resuspension rate, and superficial sedimentary OM stock). The initial full models included the following fixed factors: *site* (4 levels: S1, S2, S3, S4), *habitat* (2 levels: *Zostera noltei*, Zn, and *Sporobolus maritimus*, Sm), and *bed elevation* (continuous variable), and all their possible interactions. The final models included only the significant factors following the hierarchical principle (if an interaction factor is included in the model, the main effects are included too, even if the p-values associated with their coefficients are not significant; James et al., 2014). Tukey HSD multiple comparison tests were used to identify differences among the factor's levels. When an interaction of a categorical and numerical variable was significant, linear models were individually applied to each combination to assess the significance of the linear relationship. The significance level was $p < 0.05$ for all tests. Statistical analysis was carried with the R programming language (R version 4.0.4; R Core Team, 2021).

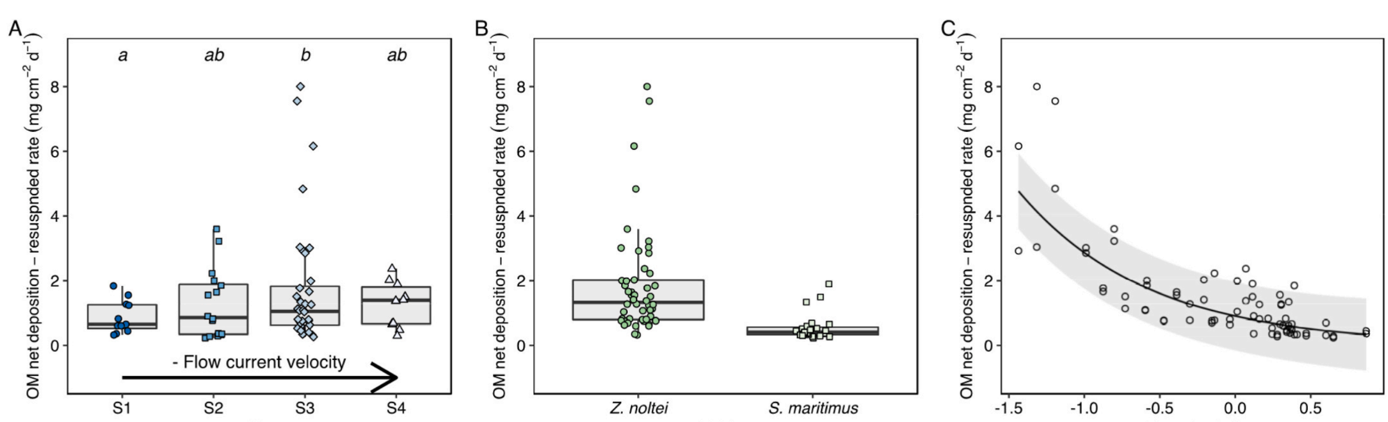

Fig. 3. Significant drivers of variation of the organic matter (OM) net deposition-resuspension rate (mg cm^{-2} d^{-1}) along the vertical intertidal distribution: (A) site, from the highest (S1) to the lowest (S4) current flow velocity; (B) habitat, from the lower intertidal seagrass *Zostera noltei* to the upper intertidal saltmarsh *Sporobolus maritimus*; and (C) bed elevation (referred to mean sea level, MSL). Different letters on boxplots in (A) indicate significant differences among sites. Line in (C) represents the multiple regression model.

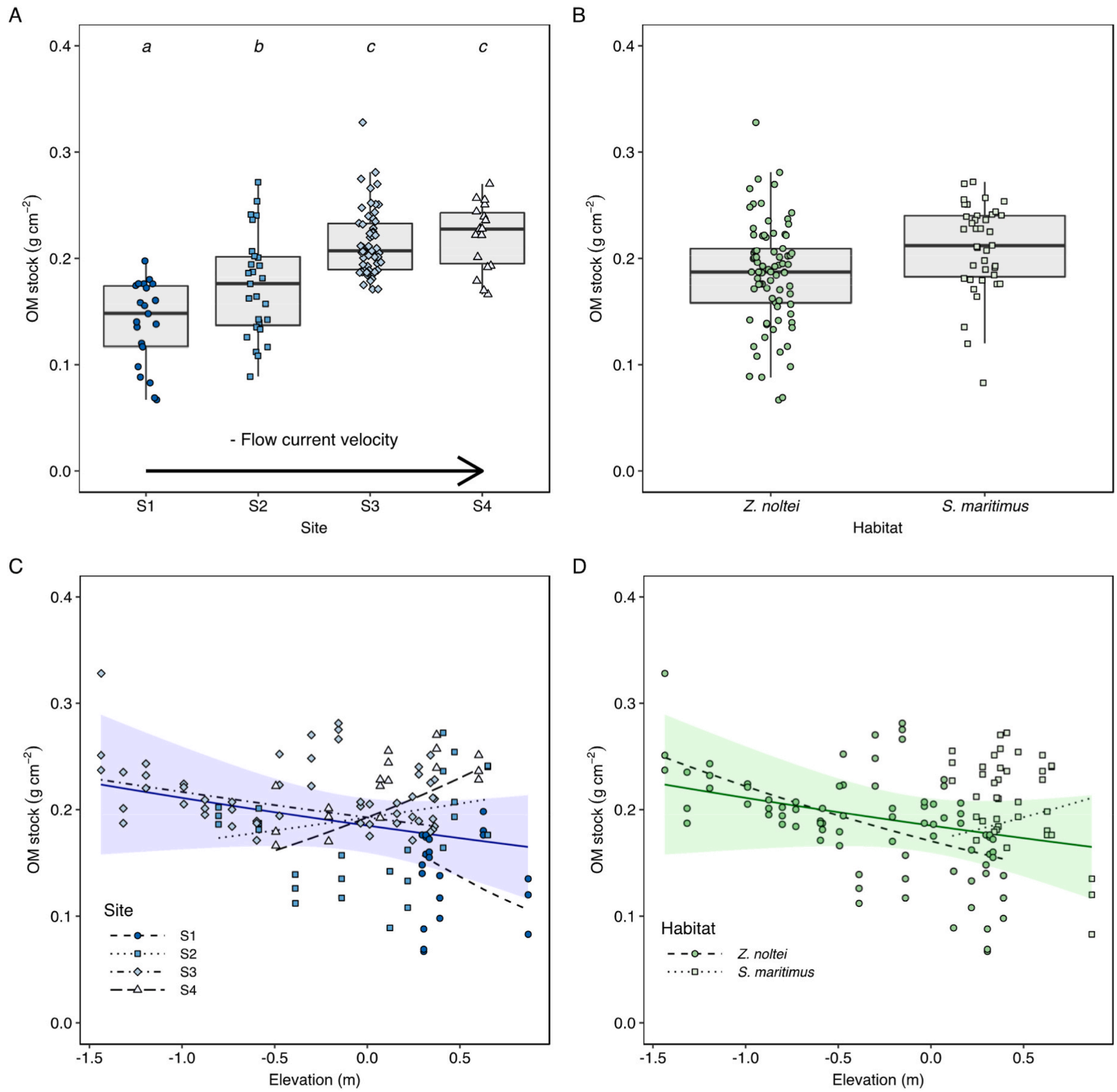

Fig. 4. Significant drivers of variation of superficial sedimentary organic matter (OM) stock (g cm^{-2}) along the vertical intertidal distribution: (A) site, from the highest (S1) to the lowest (S4) current flow velocity; (B) habitat, from the lower intertidal seagrass *Zostera noltei* to the upper intertidal saltmarsh *Sporobolus maritimus*; (C) bed elevation (referred to mean sea level, MSL) in interaction with site; and (D) bed elevation (referred to mean sea level, MSL) in interaction with habitat. Different letters of boxplots indicate significant differences among sites. Solid lines and ribbons in (C) and (D) represent the multiple regression model for the whole dataset across the entire elevation gradient. The other not solid lines shown are the statistically significant relationships observed in sites S1–S4 and for each of the habitats.

3. Results

3.1. Transect characterisation

A continuum of bed elevation from −1.44 m to 0.87 m MSL was covered with all transects, corresponding to hydroperiods ranging from 96% to 18% (Table 1). The seagrass *Z. noltei* occurred in bed elevations from −1.44 to 0.39 m MSL and hydroperiods ranging from 96% to 36%, while saltmarsh *S. maritimus* occurred in bed elevations from 0.11 to 0.87 m MSL and hydroperiods from 46% to 18%. The maximum height of the water column, i.e., water depth, over *Z. noltei* meadows ranged from 1.4 to 3.1 m, and from 1.1 to 1.6 m for *S. maritimus*. The bed slope (%) of the seagrass meadow (from 0.6 to 11.5%) was generally steeper than of the salt marsh (from 0.1 to 5%), except in site S1 where the slope of the seagrass bed was slightly lower (Table 1). Bed elevation and hydroperiod were highly, inversely correlated (Pearson's correlation coefficient = −0.999, t = −135.3, $p < 0.001$, df = 40).

3.2. Organic matter net deposition-resuspension rate and stock

The selected regression model explained 37% of the variance in the OM content of the deposited material ($F_{7,65} = 7.0$, $p < 0.001$; Table 3), including as explanatory variables *bed elevation* ($F_{1,65} = 0.1$, $p = 0.725$), *site* ($F_{3,65} = 12.1$, $p < 0.001$), and the interaction *site* × *bed elevation* ($F_{3,65} = 4.3$, $p < 0.05$), yet only *site* and *site* × *bed elevation* were significant (Fig. 2). On average, OM content was lower at site S1 (3.54 ± 0.27% dw, n = 11), than in the other sites, where OM ranged from 5.28 ± 0.36 to 5.76 ± 0.46% dw (n = 10 to 36; Fig. 2A). Bed elevation was a significant explanatory variable only in site S2 ($t_{1,34} = -2.4$, $p < 0.05$), where OM content of the deposited material increased from the low to the upper elevations, and in S3 ($t_{1,14} = 2.8$, $p < 0.01$), where the opposite pattern was observed (Fig. 2B).

OM net deposition-resuspension rate varied with *site* ($F_{3,67} = 3.1$, $p < 0.05$), *habitat* ($F_{1,67} = 107.9$, $p < 0.001$) and *bed elevation* ($F_{1,67} = 75.3$, $p < 0.001$), yet not with their interactions. The final model

Table 2
Statistical summary for organic matter content (OM, % dw) in the deposited sediment, OM net deposition-resuspension rate (g cm^{-2} d^{-1}), and superficial sedimentary OM stock (g cm^{-2}) for the co-occurring habitats of seagrass species *Zostera noltei* (Zn) and saltmarsh species *Sporobolus maritimus* (Sm) at the four sampling sites, from the highest (S1) to the lowest (S4) current flow velocity. Data are showed as the mean ± SE and as range (minimum and maximum) between brackets.

Site	Habitat	OM content deposited material (% dw)	OM net deposition-resuspension rate (mg cm^{-2} d^{-1})	OM stock (g cm^{-2})
S1	Zn	3.60 ± 0.33 (1.82–4.78)	0.99 ± 0.17 (0.32–1.84)	0.14 ± 0.01 (0.07–0.18)
	Sm	3.26 ± 0.23 (3.04–3.49)	0.40 ± 0.04 (0.36–0.44)	0.15 ± 0.02 (0.08–0.20)
S2	Zn	4.86 ± 0.42 (3.29–7.05)	1.72 ± 0.31 (0.35–3.60)	0.15 ± 0.01 (0.09–0.20)
	Sm	6.20 ± 0.57 (4.19–7.46)	0.29 ± 0.02 (0.23–0.36)	0.22 ± 0.01 (0.16–0.27)
S3	Zn	5.38 ± 0.18 (3.55–6.94)	2.23–0.42 (0.63–8.00)	0.22 ± 0.01 (0.17–0.33)
	Sm	5.09 ± 0.31 (3.38–6.28)	0.51 ± 0.10 (0.26–1.34)	0.21 ± 0.01 (0.17–0.25)
S4	Zn	5.54 ± 0.21 (5.13–6.13)	1.79 ± 0.24 (1.37–2.37)	0.20 ± 0.01 (0.17–0.23)
	Sm	5.91 ± 0.78 (3.83 ± 8.65)	0.92 ± 0.26 (0.30–1.90)	0.25 ± 0.00 (0.23–0.27)

Table 3
Models' coefficients obtained from the multiple regression analysis for the organic matter (OM) variables: OM content in the deposited material, OM net deposition-resuspension rate, and OM superficial stock. Each model considered different sources of variation. Levels of factors used as reference (in the intercept) were *site* S1 and *habitat* saltmarsh.

Source of variation	Coefficient estimate	Standard error	t value	p value
Model OM content in the deposited material (adjusted $R^2 = 0.37$, $F_{7,65} = 7.0$, $p < 0.001$)				
Intercept	1.575	0.046	33.99	<0.001
Site S2	0.324	0.159	2.04	0.046
Site S3	0.293	0.155	1.89	0.063
Site S4	0.414	0.171	2.42	0.018
Bed elevation	−0.005	0.105	−0.05	0.962
Site S2 x Bed elevation	0.540	0.334	1.62	0.111
Site S3 x Bed elevation	0.086	0.320	0.27	0.789
Site S4 x Bed elevation	0.157	0.402	0.39	0.697
Model OM net deposition-resuspension rate (adjusted $R^2 = 0.72$, $F_{5,67} = 38.5$, $p < 0.001$)				
Intercept	−0.024	0.067	−0.35	0.723
Site S2	0.223	0.135	1.65	0.103
Site S3	−0.217	0.099	−2.19	0.032
Site S4	−0.347	0.095	−3.64	<0.001
Habitat seagrass	−0.102	0.082	−1.25	0.216
Bed elevation	−1.285	0.148	−8.68	<0.001
Model OM superficial stock (adjusted $R^2 = 0.59$, $F_{11,108} = 16.9$, $p < 0.001$)				
Intercept	0.227	0.013	17.39	<0.001
Site S2	0.057	0.038	1.49	0.138
Site S3	−0.033	0.014	−2.41	0.018
Site S4	−0.016	0.013	−1.22	0.224
Habitat seagrass	0.034	0.007	5.21	<0.001
Bed elevation	−0.079	0.025	−3.13	0.002
Site S2 x Habitat seagrass	0.027	0.016	1.65	0.102
Site S3 x Habitat seagrass	0.024	0.009	2.55	0.012
Site S4 x Habitat seagrass	−0.034	0.008	−4.21	<0.001
Site S2 x Bed elevation	−0.183	0.071	−2.59	0.011
Site S3 x Bed elevation	0.016	0.028	0.56	0.573
Site S4 x Bed elevation	0.065	0.026	2.48	0.015

explained 72% of the variance ($F_{5,67} = 38.5$, $p < 0.001$; Table 3). The net deposition-resuspension rate of OM differed only between sites S1 and S3, being slightly lower at S1 (0.88 ± 0.15 mg cm^{-2} d^{-1}, n = 11; $p < 0.05$; Fig. 3A). OM net deposition-resuspension rate was more than 3-fold higher at the seagrass meadows (1.86 ± 0.24 mg cm^{-2} d^{-1}, n = 50) than at the salt marsh (0.56 ± 0.09 mg cm^{-2} d^{-1}, n = 23; Fig. 3B), and it was inversely and exponentially related to bed elevation, following the vertical gradient of decreasing hydroperiod (Fig. 3C).

OM superficial sedimentary stock was best explained when including the factors *site* ($F_{3,108} = 39.8$, $p < 0.001$), *habitat* ($F_{1,108} = 13.4$, $p < 0.001$), *bed elevation* ($F_{1,108} = 10.8$, $p < 0.01$), and the interactions *site* × *habitat* ($F_{3,108} = 9.6$, $p < 0.001$) and *site* × *bed elevation* ($F_{3,108} = 4.6$, $p < 0.01$). This model explained 59% of variance of the OM superficial stock ($F_{11,108} = 16.9$, $p < 0001$; Table 3). On average, the OM stock increased 1.5-fold from S1 (0.14 ± 0.01 g OM cm^{-2}, n = 21) to S4 (0.22 ± 0.01 g OM cm^{-2}, n = 21; Fig. 4A), and it was slightly higher in the salt marsh (0.21 ± 0.01 g OM cm^{-2}, n = 39) than in the seagrass meadows (0.19 ± 0.01 g OM cm^{-2}, n = 81; Table 2, Fig. 4B). Considering the entire studied elevation gradient, the OM superficial sedimentary stock decreased exponentially with bed elevation (blue solid line in Fig. 4C). However, this variation differed between sites (increasing in S2 and S4, and decreasing in S1 and S3; Fig. 4C) and habitats (decreasing in the seagrass meadows and increasing in the saltmarsh; Fig. 4D).

4. Discussion

We showed here that two vectors of spatial variation need to be considered to describe the intertidal sedimentary OM stocks of Ria Formosa lagoon: the bed elevation that imposes a decrease of the hydroperiod and the change of habitat from the lower seagrass *Z. noltei* to the upper saltmarsh *S. maritimus*, and the horizontal spatial variation along the secondary channels of the lagoon that imposes a decrease in the flow current velocity (Fig. 5). The biophysical drivers associated to both spatial vectors determined the overall vertical decrease of OM stocks at higher bed elevations (yet with variation among sites and habitats), and their horizontal increase with decreasing flow velocity magnitude along secondary channels (Fig. 5). Importantly, we found that the variation of the OM stocks with bed elevation was exponential. A multiple regression model, which explained 59% of the observed variation based on bed elevation, hydrodynamic exposure, and habitat type, is suggested to predict the superficial sedimentary stocks of OM in the vegetated intertidal habitats of the Ria Formosa lagoon.

The input of OM into the vegetated intertidal habitats and the OM content of deposited material determine to a lager extent the sediment OM stocks. The OM net deposition-resuspension rates varied vertically, being higher in the lower intertidal areas colonised by seagrass *Z. noltei* where submersion time is longer, as opposed to the upper intertidal areas where saltmarsh *S. maritimus* develops, which are less frequently inundated. The same variation pattern was previously described in intertidal habitats of Ria Formosa lagoon, including the seagrass *Z. noltei*, the saltmarsh *S. maritimus* and bare sediment (Neumeier and Ciavola, 2004). Hydroperiod is an obvious factor to explain the variation with bed elevation since deposition only occurs in submerged conditions. The spatial variation of OM deposition is also related to hydrodynamics, since a higher deposition of fine particles containing more OM occurs in sheltered than in exposed sites (Keil and Mayer, 2014). Indeed, OM deposition varied along the flow velocity gradient, with more OM in the most sheltered sites. A similar pattern in the variation of particulate OM content in the water column of Ria Formosa lagoon was previously reported, with an increase of 75% in the OM content from the inlet zone to the inner part of the lagoon, along the main navigation channel (Machás and Santos, 1999). Likely, the distance from the OM sources can also explain this pattern, since sheltered locations, being close to the mainland, may receive more OM from land runoff or wastewater discharges (Cabaço et al., 2008).

The horizontal variation of sedimentary OM and organic carbon stocks along decreasing flow velocities was previously reported in the same system, for the superficial (Santos et al., 2019) and the top meter sediment layer (Martins et al., 2021), with increases between two- and fourfold. The effect of hydrodynamics, in the form of currents or waves,

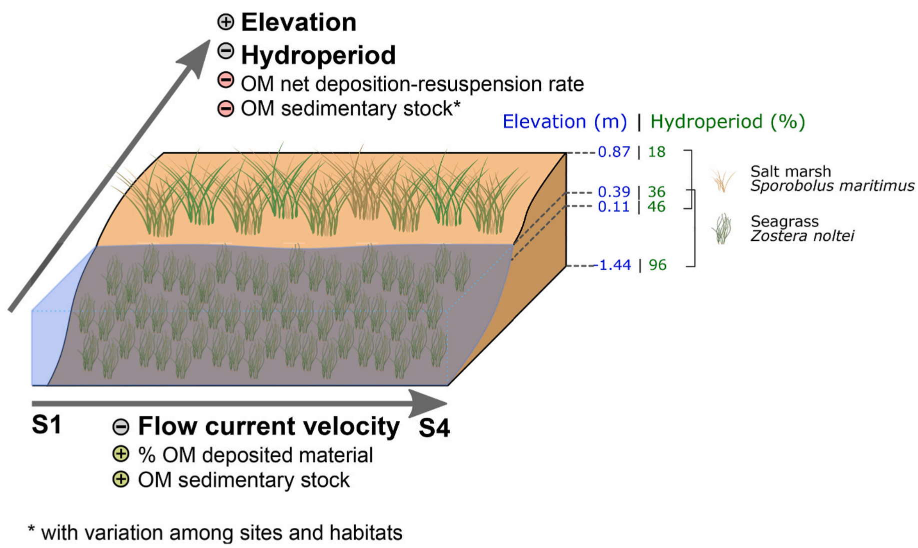

Fig. 5. Summary of the general results explaining the spatial variability in the organic matter (OM) net deposition-resuspension rate and superficial sedimentary stock in the Ria Formosa across bed elevation and flow current velocity gradients (from the highest S1 to the lowest S4 current flow velocity) and between two co-occurring intertidal vegetated habitats (seagrass *Zostera noltei* and saltmarsh *Sporobolus maritimus*). Ranges of bed elevation are given in m MSL and hydroperiod in percentage of monthly submersion time (for March 2017). Direction of the variation is given by symbols + (increase) and – (decrease).

on the sedimentary OM stocks (and hence organic carbon stocks) is widely accepted (Kelleway et al., 2016; Röhr et al., 2016; Samper-Villarreal et al., 2016; Serrano et al., 2016; Macreadie et al., 2017; Mazarrasa et al., 2018; Oreska et al., 2017; Dahl et al., 2018, 2020; Kindeberg et al., 2018; Santos et al., 2019; Martins et al., 2021). The low contents of OM in the deposited material at the site subjected to the highest velocities (S1) is reflected too in the small OM stock of the superficial sediment in the same site. This can be explained by the relationship between the sediment particle size and flow current velocity, since fine sediments (clay and silt), which are the fractions that can adhere more OM, accumulate at lower rates in areas experiencing high velocities (e.g., Santos et al., 2019). The vertical variation of OM stocks is also supported by observations in other coastal systems, including mangrove forests which are located at higher elevations than seagrasses (Ewers-Lewis et al., 2018, 2020; García-Bonet et al., 2019). Yet, other studies did not find differences among low intertidal seagrasses and upper salt marshes in three Australian estuaries (Conrad et al., 2019). A common trend in sediment grain size distribution with bed elevation is the fining of the sediment landward (Yang et al., 2008). Particularly in the Ria Formosa, mean grain size at upper saltmarsh was found to be smaller than at the lower intertidal seagrass meadows (Santos et al., 2019). Thus, based only on the grain size distribution, we could expect larger OM stocks at higher elevations than at lower, and accordingly we observed larger stocks at the saltmarsh than at the seagrass meadows. Yet, within the seagrass meadow, OM stock decreased landward, and this could be more related to the hydroperiod than with the grain size. An important finding of our study was the exponential nature of the variation of OM short-term deposition and in the OM stocks with bed elevation. This finding reinforces the idea of considering non-linearity, thresholds and limiting functions in the natural processes and, specifically in ecosystem service assessment (Koch et al., 2009).

There are multiple processes that likely explain the observed spatial pattern distribution, related not only to primary OM input, but also to post-deposition processes such as resuspension, mineralization and burial, some of them acting in opposite directions: 1) with increasing bed elevation, net deposition-resuspension rate is reduced due to shorter hydroperiods, so that the primary OM input is lower in higher parts of the profile, especially in the salt marsh; 2) at the same time, with increasing bed elevation, we expect a reduction in the current velocity, which may enhance the deposition of the finest fraction of the suspended sediments, which have large mineral-specific surface areas; 3) the decrease in current velocity with increasing bed elevation, within the same or through the connected habitats, makes the upper part of the intertidal area experience less resuspension (Friend et al., 2003); 4) with increasing bed elevation and decreasing hydroperiod, intertidal sediments are exposed for longer periods to air, and therefore to a rise in temperature and direct light, which contribute to the OM remineralization of the organic matter (Vale et al., 1992; Hedges and Keil, 1995; Keil and Mayer, 2014); and finally, 5) the sources of the OM, which are also affected by the hydrodynamics (Santos et al., 2019; Martins et al., 2021) can also determine their preservation and remineralization.

This study highlights that both vertical and horizontal vectors of spatial variation must be included in spatial models of blue carbon stocks in mesotidal systems with relevant gradients of flow current velocity (Fig. 5). We conclude that bed elevation is a necessary driver to estimate carbon stocks in a more precise way, yet it cannot be used as a stand-alone or main predictor. In a model built to estimate blue carbon stocks in sediments of south-eastern Australia, which explained 46% of the variability in 30 cm deep sediment C stocks, the ecological variables were the most important factors and bed elevation was ranked as a secondary factor (Ewers Lewis et al., 2020). Our model for the OM superficial sedimentary stock explained about 59% of the variation found. This means that there are other environmental factors not included in our study that are responsible to explain the missing 41% of spatial variation. Among them, distance to the source or biophysical factors that control processes such as retention, exportation and remineralization of the deposited OM, could contribute to further explain the observed spatial variability. Despite the remaining variation to be explained, local blue carbon estimation based on these relatively easy-to-get variables, flow current velocity from hydrodynamical models and bed elevation from digital elevation models, would improve the accuracy of the present inventories of blue carbon stocks in tidal lagoons. In addition, further studies should include temporal variation, such as variation in tidal ranges (neap and spring tides) and seasonality for a better understanding of the deposition patterns, since our study was based on measurements during spring tides in a specific time.

CRediT authorship contribution statement

Carmen B. de los Santos: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Visualization, Writing – original draft. **François Lahuna:** Investigation, Methodology, Writing – review & editing. **André Silva:** Investigation, Methodology, Writing – review & editing. **Cátia Freitas:** Investigation, Writing – review & editing. **Márcio Martins:** Investigation, Writing – review & editing. **A. Rita Carrasco:** Investigation, Methodology, Resources, Writing – review & editing. **Rui Santos:** Conceptualization, Funding acquisition, Methodology, Resources, Writing – review & editing.

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.

Acknowledgments

This study received Portuguese national funds from FCT - Foundation for Science and Technology (grant numbers UIDB/04326/2020, PTDC/MAR-EST/3223/2014, SFRH/BPD/119344/2016, 2020.03825.CEECIND, DL57/2016/CP1361/CT0002, and 2020.06996.BD).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2022.107896.

References

Nepf, H.M., Sullivan, J.A., Zavistoski, R.A., 1997. A model for diffusion within emergent vegetation. Limnol. Oceanogr. 42 (8), 1735–1745.
Bockelmann, A.C., Bakker, J.P., Neuhaus, R., Lage, J., 2002. The relation between vegetation zonation, elevation and inundation frequency in a Wadden Sea salt marsh. Aquat. Bot. 73 (3), 211–221.
Butzeck, C., Eschenbach, A., Gröngröft, A., Hansen, K., Nolte, S., Jensen, K., 2015. Sediment deposition and accretion rates in tidal marshes are highly variable along estuarine salinity and flooding gradients. Estuar. Coast 38 (2), 434–450.
Cabaço, S., Machás, R., Vieira, V., Santos, R., 2008. Impacts of urban wastewater discharge on seagrass meadows (*Zostera noltii*). Estuar. Coast Shelf Sci. 78 (1), 1–13.
Cahoon, D.R., Reed, D.J., 1995. Relationships among marsh surface topography, hydroperiod, and soil accretion in a deteriorating Louisiana salt marsh. J. Coast Res. 357–369.
Carrasco, A.R., Plomaritis, T., Reyns, J., Ferreira, Ó., Roelvink, D., 2018. Tide circulation patterns in a coastal lagoon under sea-level rise. Ocean Dynam. 68 (9), 1121–1139.
Chmura, G.L., Anisfeld, S.C., Cahoon, D.R., Lynch, J.C., 2003. Global carbon sequestration in tidal, saline wetland soils. Global Biogeochem. Cycles 17 (4).
Christiansen, T., Wiberg, P.L., Milligan, T.G., 2000. Flow and sediment transport on a tidal salt marsh surface. Estuar. Coast Shelf Sci. 50 (3), 315–331.
Conrad, S., Brown, D.R., Alvarez, P.G., Bates, B., Ibrahim, N., Reid, A., Sanders, C.J., 2019. Does regional development influence sedimentary blue carbon stocks? A case study from three Australian estuaries. Front. Mar. Sci. 518. https://doi.org/10.3389/fmars.2018.00518.
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 (6), 2793–2805.
Dahl, M., Asplund, M.E., Deyanova, D., Franco, J.N., Koliji, A., Infantes, E., Perry, D., Björk, M., Gullström, M., 2020. High seasonal variability in sediment carbon stocks of cold-temperate seagrass meadows. J. Geophys. Res.: Biogeosciences 125 (1), e2019JG005430.
de los Santos, C.B., Martins, M., 2021. R Code to Estimate Water Depth and Hydroperiod Based on Tide Height and Bed Elevation. Zenodo. https://doi.org/10.5281/zenodo.4642874, Version v1.0.2.
de los Santos, C.B., Krause-Jensen, D., Alcoverro, T., Marbà, N., Duarte, C.M., et al., 2019. Recent trend reversal for declining European seagrass meadows. Nat. Commun. 10, 3356.
Deegan, L.A., Johnson, D.S., Warren, R.S., Peterson, B.J., Fleeger, J.W., Fagherazzi, S., Wollheim, W.M., 2012. Coastal eutrophication as a driver of salt marsh loss. Nature 490 (7420), 388–392.
Dias, J.M., Sousa, M.C., 2009. Numerical modeling of Ria Formosa tidal dynamics. J. Coast Res. 1345–1349.
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. Global Change Biol.
Ewers Lewis, C.J., Carnell, P.E., Sanderman, J., Baldock, J.A., Macreadie, P.I., 2018. Variability and vulnerability of coastal 'blue carbon' stocks: a case study from southeast Australia. Ecosystems 21 (2), 263–279.
Ewers Lewis, C.J., Young, M.A., Ierodiaconou, D., Baldock, J.A., Hawke, B., et al., 2020. Drivers and modelling of blue carbon stock variability in sediments of south-eastern Australia. Biogeosciences 17, 2041–2059.
Ford, H., Garbutt, A., Duggan-Edwards, M., Pagès, J.F., Harvey, R., Ladd, C., Skov, M.W., 2019. Large-scale predictions of salt-marsh carbon stock based on simple observations of plant community and soil type. Biogeosciences 16 (2), 425–436.
French, J.R., Spencer, T., Murray, A.L., Arnold, N.S., 1995. Geostatistical analysis of sediment deposition in two small tidal wetlands, Norfolk, UK. J. Coast Res. 308–321.
Friend, P.L., Ciavola, P., Cappucci, S., Santos, R., 2003. Bio-dependent bed parameters as a proxy tool for sediment stability in mixed habitat intertidal areas. Continent. Shelf Res. 23, 1899–1917.
Garcias-Bonet, N., Delgado-Huertas, A., Carrillo-de-Albornoz, P., Anton, A., Almahasheer, H., Marbà, N., Hendriks, I.E., Krause-Jensen, D., Duarte, C.M., 2019. Carbon and nitrogen concentrations, stocks, and isotopic compositions in Red Sea seagrass and mangrove sediments. Front. Mar. Sci. 6, 267.
Hansen, K., Butzeck, C., Eschenbach, A., Gröngröft, A., Jensen, K., Pfeiffer, E.M., 2017. Factors influencing the organic carbon pools in tidal marsh soils of the Elbe estuary (Germany). J. Soils Sediments 17 (1), 47–60.
Hedges, J.I., Keil, R.G., 1995. Sedimentary organic matter preservation: an assessment and speculative synthesis. Mar. Chem. 49 (2–3), 81–115.
Howard, J., Hoyt, S., Isensee, K., Telszewski, M., Pidgeon, E., 2019. Coastal Blue Carbon: Methods for Assessing Carbon Stocks and Emissions Factors in Mangroves, Tidal Salt Marshes, and Seagrasses. International Union for Conservation of Nature.
IPCC, 2019. Climate Change and Land: an IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse Gas Fluxes in Terrestrial Ecosystems.
IPCC, 2014. In: Hiraishi, T., Krug, T., Tanabe, K., Srivastava, N., Baasansuren, J., Fukuda, M., Troxler, T.G. (Eds.), 2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands. IPCC, Switzerland. Published.
Jacob, J., Cardeira, S., Rodrigues, M., Bruneau, N., Azevedo, A., Fortunato, A.B., Rosa, M., Cravo, A., 2013. Experimental and numerical study of the hydrodynamics of the western sector of Ria Formosa. J. Coast Res. (65), 2011–2016.
James, G., Witten, D., Hastie, T., Tibshirani, R., 2014. An Introduction to Statistical Learning: with Applications in R. Springer Publishing Company, Incorporated.
Jiménez-Arias, J.L., Morris, E., Rubio-de-Inglés, M.J., Peralta, G., García-Robledo, E., Corzo, A., Papaspyrou, S., 2020. Tidal elevation is the key factor modulating burial rates and composition of organic matter in a coastal wetland with multiple habitats. Sci. Total Environ. 724, 138205.
Keil, R.G., Mayer, L.M., 2014. Mineral matrices and organic matter. In: Holland, H.D., Turekian, K.K. (Eds.), Treatise on Geochemistry, second ed., vol. 12. Elsevier, Oxford, pp. 340–346.
Kelleway, J.J., Saintilan, N., Macreadie, P.I., Ralph, P.J., 2016. Sedimentary factors are key predictors of carbon storage in SE Australian saltmarshes. Ecosystems 19 (5), 865–880.
Kelleway, J.J., Saintilan, N., Macreadie, P.I., Baldock, J.A., Ralph, P.J., 2017. Sediment and carbon deposition vary among vegetation assemblages in a coastal salt marsh. Biogeosciences 4 (16), 3763–3779.
Kindeberg, T., Ørberg, S.B., Röhr, M.E., Holmer, M., Krause-Jensen, D., 2018. Sediment stocks of carbon, nitrogen, and phosphorus in Danish eelgrass meadows. Front. Mar. Sci. 5, 474.
Koch, E.W., Barbier, E.B., Silliman, B.R., Reed, D.J., Perillo, G.M., Hacker, S.D., Granek, E.F., Primavera, J.H., Muthiga, N., Polasky, S., Halpern, B.S., Kennedy, C.J., Kappel, C.V., Wolanski, E., 2009. Non-linearity in ecosystem services: temporal and spatial variability in coastal protection. Front. Ecol. Environ. 7 (1), 29–37.
Leonard, L.A., 1997. Controls of sediment transport and deposition in an incised mainland marsh basin, southeastern North Carolina. Wetlands 17 (2), 263–274.
Leonard, L.A., Luther, M.E., 1995. Flow hydrodynamics in tidal marsh canopies. Limnol. Oceanogr. 40 (8), 1474–1484.
Lima, M.D.A.C., Ward, R.D., Joyce, C.B., 2020. Environmental drivers of sediment carbon storage in temperate seagrass meadows. Hydrobiologia 847 (7), 1773–1792.
Machás, R., Santos, R., 1999. Sources of organic matter in Ria Formosa revealed by stable isotope analysis. Acta Oecol. 20 (4), 463–469.
Macreadie, P.I., Ollivier, Q.R., Kelleway, J.J., Serrano, O., Carnell, P.E., Ewers Lewis, C., Atwood, T.B., Sanderman, J., Baldock, J., Connolly, R.M., Duarte, C.M., Lavery, P.S., Lovelock, C.E., 2017. Carbon sequestration by Australian tidal marshes. Sci. Rep. 7, 44071.
Macreadie, P.I., Anton, A., Raven, J.A., Beaumont, N., Connolly, et al., 2019. The future of Blue Carbon science. Nat. Commun. 10 (1), 1–13.
Malta, E.J., Stigter, T.Y., Pacheco, A., Dill, A.C., Tavares, D., Santos, R., 2017. Effects of external nutrient sources and extreme weather events on the nutrient budget of a southern European coastal lagoon. Estuar. Coast 40 (2), 419–436.
Martins, M., de los Santos, C.B., Masqué, P., Carrasco, A.R., Veiga-Pires, C., Santos, R., 2021. Carbon and nitrogen stocks and burial rates in intertidal vegetated habitats of a mesotidal coastal lagoon. Ecosystems 1–15.
Mateo, M.A., Cebrián, J., Dunton, K., Mutchler, T., 2006. Carbon flux in seagrass ecosystems. In: *Seagrasses: Biology, Ecology and Conservation* 159–192. Springer-Verlag.
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.
Möller, I., Christie, E., 2019. Hydrodynamics and modeling of water flow in coastal wetlands. In: Coastal Wetlands. Elsevier, pp. 289–323.
Nellemann, C., Corcoran, E. (Eds.), 2009. Blue Carbon: the Role of Healthy Oceans in Binding Carbon: a Rapid Response Assessment. UNEP/Earthprint.
Neumeier, U., Ciavola, P., 2004. Flow resistance and associated sedimentary processes in a *Spartina maritima* salt-marsh. J. Coast Res. 20, 435–447.
Novak, A.B., Pelletier, M.C., Colarusso, P., Simpson, J., Gutierrez, M.N., Arias-Ortiz, A., Charpentier, M., Masqué, P., Vella, P., 2020. Factors influencing carbon stocks and accumulation rates in eelgrass meadows across New England, USA. Estuar. Coast 1–16.
Oreska, M.P., McGlathery, K.J., Porter, J.H., 2017. Seagrass blue carbon spatial patterns at the meadow-scale. PLoS One 12 (4), e0176630.
Ouyang, X., Lee, S.Y., 2014. Updated estimates of carbon accumulation rates in coastal marsh sediments. Biogeosciences 5057.
Pennings, S.C., Callaway, R.M., 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. Ecology 73 (2), 681–690.
Pham, T.D., Xia, J., Ha, N.T., Bui, D.T., Le, N.N., Tekeuchi, W., 2019. A review of remote sensing approaches for monitoring blue carbon ecosystems: mangroves, seagrasses,

and salt marshes during 2010‑2018. Sensors 19 (8), 1933. https://doi.org/10.3390/s19081933.

R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ricart, A.M., York, P.H., Bryant, C.V., Rasheed, M.A., Ierodiaconou, D., Macreadie, P.I., 2020. High variability of Blue Carbon storage in seagrass meadows at the estuary scale. Sci. Rep. 10 (1), 1–12.

Röhr, M.E., Boström, C., Canal-Vergés, P., Holmer, M., 2016. Blue carbon stocks in Baltic Sea eelgrass (Zostera marina) meadows. Biogeosciences 13 (22), 6139–6153. https://doi.org/10.5194/bg-13-6139-2016.

Samper-Villarreal, J., Lovelock, C.E., Saunders, M.I., Roelfsema, C., Mumby, P.J., 2016. Organic carbon in seagrass sediments is influenced by seagrass canopy complexity, turbidity, wave height, and water depth. Limnol. Oceanogr. 61 (3), 938–952.

Santos, R., Duque-Núñez, N., de los Santos, C.B., Martins, M., Carrasco, A.R., Veiga-Pires, C., 2019. Superficial sedimentary stocks and sources of carbon and nitrogen in coastal vegetated assemblages along a flow gradient. Sci. Rep. 9 (1), 610.

Serrano, O., Ricart, A.M., Lavery, P.S., Mateo, M.A., Arias-Ortiz, A., Masque, P., Rozaimi, M., Steven, A., Duarte, C.M., 2016. Key biogeochemical factors affecting soil carbon storage in Posidonia meadows. Biogeosciences 13 (15), 4581–4594.

Silva, J., Santos, R., 2003. Daily variation patterns in seagrass photosynthesis along a vertical gradient. Mar. Ecol.: Prog. Ser. 257, 37–44.doi. https://doi.org/10.3354/meps257037.

Vale, C., Hussenot, J., Falcão, M., Martin, J.-L., 1992. Dawn-dusk chemical variations near the sediment-water interface of a clam-growth bank of Ria Formosa. Boletim INIP 19, 71–79.

Yang, S.L., Li, H., Ysebaert, T., Bouma, T.J., Zhang, W.X., Wang, Y.Y., Li, P., Li, M., Ding, P.X., 2008. Spatial and temporal variations in sediment grain size in tidal wetlands, Yangtze Delta: on the role of physical and biotic controls. Estuar. Coast Shelf Sci. 77 (4), 657–671.

Zhang, T., Chen, H., Cao, H., Ge, Z., Zhang, L., 2017. Combined influence of sedimentation and vegetation on the soil carbon stocks of a coastal wetland in the Changjiang estuary. Chin. J. Oceanol. Limnol. 35 (4), 833–843.