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Quantification of blue carbon stocks associated with *Posidonia oceanica seagrass meadows* in Corsica (NW Mediterranean)

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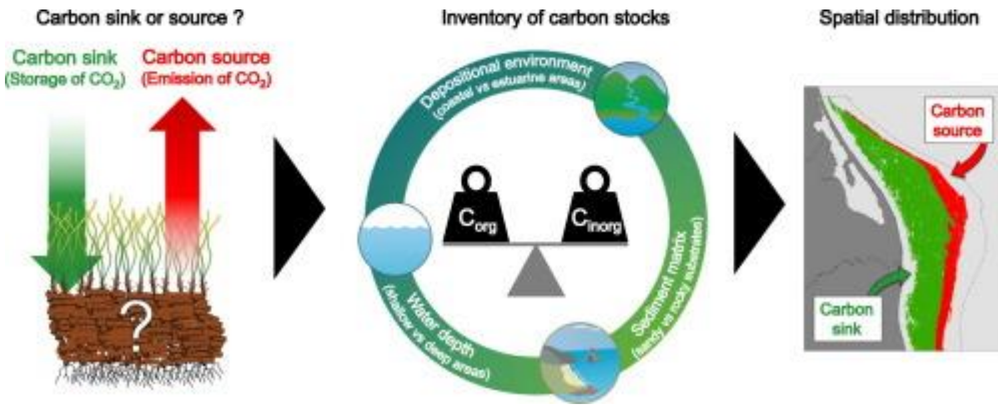
Abstract :

In the last decades, the increasing necessity to reduce atmospheric carbon dioxide (CO2) concentrations has intensified interest in quantifying the capacity of coastal ecosystems to sequester carbon, referred to commonly as 'Blue Carbon' (BC). Among coastal habitats, seagrass meadows are considered as natural carbon sinks due to their capacity to store large amounts of carbon in their sediments over long periods of time. However, the spatial heterogeneity of carbon stocks in seagrass sediments needs to be better understood to improve the accuracy of BC assessments, particularly where there is high environmental variability. In the Mediterranean, Posidonia oceanica (L.) Delile constitutes extensive meadows considered as long-term carbon sinks due to the development of an exceptional structure known as 'matte', reaching several meters in height, which can be preserved over millennia. In order to specify the role of P. oceanica meadows in climate change mitigation, an estimate of carbon stocks has been conducted along the eastern coast of Corsica (NW Mediterranean). The approach is mainly based on the biogeochemical analysis of 39 sediment cores. Organic carbon (Corg; 327 ± 150 t ha−1, mean ± SE) and inorganic carbon stocks (Cinorg; 245 ± 45 t ha−1) show a high variability related to water depth, matrix (sandy vs rocky substrate) or the depositional environment (coastal vs estuary). The isotopic signature (δ13C) revealed a substantial contribution of allochthonous inputs of organic matter (macroalgae and sestonic sources) mainly in estuarine environment and shallow areas. The carbon stocks in the first 250 cm of matte (average thickness) were estimated at 5.6–14.0 million t Corg (study site) and 14.6–36.9 million t Corg (Corsica), corresponding to 11.6–29.2 and 30.4–76.8 years of CO2 emissions from the population of Corsica.

Graphical abstract



Highlights

► Quantification of organic (C_{org}) and inorganic carbon (C_{inorg}) stocks is performed. ► Use of seafloor DEM provide reliable information to estimate the global stock. ► C_{org} and C_{inorg} stocks are crucial to assess the seagrass contribution as sink-source. ► For the first time, the carbon sink-source role of seagrass is modeled over 20,000 ha.

Keywords : Posidonia oceanica, Seagrass, Carbon stock, Climate change mitigation, Corsica, Mediterranean Sea

1. Introduction

The implementation of reduction strategies for atmospheric greenhouse gas (GHG) and notably carbon dioxide (CO_2) is a crucial step for meeting the objectives of the Paris Agreement (UNFCCC, 2016) and for climate change mitigation. In the last decades, the emission reduction strategy instigated to reduce CO_2 concentrations and mitigate climate change have combined the reduction of anthropogenic emission sources with nature-based approaches promoting the conservation and restoration of the world's ecosystems recognized as major natural CO_2 sinks (Herr *et al*., 2017). Among them, 'Blue Carbon' initiatives have been dedicated to the protection and the restoration of coastal and marine vegetated ecosystems contributing to the sequestration and the storage of organic carbon, referred to commonly as 'Blue Carbon' (BC) (Laffoley and Grimsditch, 2009; Nellemann *et al*., 2009). Coastal vegetated ecosystems, mainly tidal marshes, mangrove forests and seagrass meadows, are particularly effective in the capture of CO_2 and its sequestration as organic carbon in their sediments for long periods of time (Duarte *et al*., 2005). The organic carbon sequestration rates in the soils of BC ecosystems are 30- to 50-fold more effective than those of many terrestrial ecosystems (Mcleod *et al*., 2011; Duarte *et al*., 2013), contributing to the storage of large amounts of carbon and the formation of significant carbon deposits (Chmura *et al*., 2003; Fourqurean *et al*., 2012; Atwood *et al*., 2017).

Seagrass meadows occur in a wide range of habitat types (from marine to estuarine and lagoonal environments) along the shores of all continents except Antarctica, from intertidal and shallow waters to maximum depths of up to 50 m (Hemminga and Duarte, 2000; Carruthers *et al*., 2007). Seagrass meadows are highly productive ecosystems (Duarte and Chiscano, 1999) and provide key ecological functions and services of high value in comparison with other marine and terrestrial habitats (Costanza *et al*., 1997). Since the early 1980s, these ecosystems have been recognized as accumulating amounts of organic carbon (C_{org}) of potential global significance (Smith, 1981). In the context of climate change mitigation, the necessity of reducing CO_2 concentrations has intensified interest in quantifying the capacity of seagrass meadows to store C_{org} (Duarte *et al*., 2005, 2010, 2013; Mcleod *et al*., 2011; Fourqurean *et al*., 2012; Serrano *et al*., 2012, 2014, 2016a, 2016b; Lavery *et al*., 2013; Miyajima *et al*., 2015; Gullström *et al*., 2018). Although seagrass meadows occupy a relatively small area of the ocean's surface area (~0.2%; 160 000-600 000 km^2; McKenzie *et al*., 2020), their C_{org} accumulation rates range from 48 to 112 Tg C_{org} yr^{-1} representing almost 10-18% of the total carbon burial in the ocean sediment (Duarte *et al*., 2005, 2013; Kennedy *et al*., 2010; Mcleod *et al*., 2011). Through their high C_{org} burial rates, seagrass ecosystems worldwide constitute large organic carbon stocks estimated in the top meter of sediment from 4.2 to 8.4 Pg C_{org} (Fourqurean *et al*., 2012). Unlike most terrestrial ecosystems where C_{org} stocks are mainly found in living biomass and preserved for decades or centuries (*i.e.,* forests), the C_{org} stored by seagrass meadows in their sediments could be preserved over millennia (Mateo *et al*., 1997; Nellemann *et al*., 2009; Serrano *et al*., 2012;

Howard *et al.*, 2014a). The long-term carbon sinks constituted by seagrass meadows result from both the direct accumulation in the sediment matrix of C_{org} from autochthonous sources (*i.e.* seagrass belowground tissues and detritus) and allochthonous sources (*i.e.* macroalgae, epiphytes and suspended particulate organic matter – SPOM, terrestrial inputs) (Gacia and Duarte, 2001; Kennedy *et al.*, 2010).

The sequestration and the preservation of C_{org} over long time periods in seagrass soils is mainly related to (i) the seagrass meadow productivity and biomass accumulation, (ii) the sediment accretion rates resulting from the trapping of fine allochthonous particles by seagrass canopies, (iii) the biogeochemical composition and the proportion of degradation-resistant organic compounds stored (*e.g.* lignin and cellulose), and (iv) the anoxic conditions promoting slow microbial decomposition in the sediments (Klap *et al.*, 2000; Mateo *et al.*, 2006; Hendriks *et al.*, 2008; Serrano *et al.*, 2016b; Mazarrasa *et al.*, 2018). The research efforts undertaken have demonstrated a high variability in the accumulation and storage of C_{org} in seagrass ecosystems worldwide (Lavery *et al.*, 2013; Miyajima *et al.*, 2015; Mazarrasa *et al.*, 2017; Piñeiro-Juncal *et al.*, 2021), associated with the interaction of multiple biotic and abiotic factors (Belshe *et al.*, 2017; Mazarrasa *et al.*, 2021) such as seagrass species characteristics (*e.g.* density, cover and biomass productivity; Lavery *et al.*, 2013; Miyajima *et al.*, 2015; Serrano *et al.*, 2016b), water depth and light availability (*e.g.* Mateo *et al.*, 1997; Serrano *et al.*, 2014, 2016b), hydrodynamic exposure and turbidity (*e.g.* Samper-Villareal *et al.*, 2016; Mazarrasa *et al.*, 2017), geomorphological settings (*i.e.* landscape configurations; Ricart *et al.*, 2015, 2017; Gullström *et al.*, 2018) and depositional environments (*i.e.* fluvial inputs; Kennedy *et al.*, 2010; Ricart *et al.*, 2020).

The recognition of seagrass meadows as carbon sinks in coastal areas has focused efforts on quantifying their capacity to sequester and store C_{org}. However, inorganic carbon (C_{inorg}) provided by calcifying organisms associated with seagrass habitats and buried in their sediments represents a substantial carbon stock which may exceed C_{org} (Mazarrasa *et al*., 2015). The production of C_{inorg} through the calcification process may represent a source of CO_2 for the atmosphere, with a ratio of ~0.6 mol of CO_2 emitted per mol of $CaCO_3$ precipitated (Ware *et al*., 1992; Frankignoulle *et al*., 1994; Gattuso *et al*., 1998; Smith, 2013). Recently, seagrass meadows have also been highlighted for the significant sequestration of C_{inorg} imported from adjacent ecosystems such as coral reefs or terrestrial lithogenic sources (Saderne *et al*., 2019). The global annual burial of $CaCO_3$ in seagrass sediments ranging between 12 and 62 Tg C_{inorg} yr^{-1} is mainly supported by tropical meadows (~90%; Saderne *et al*., 2019) and constitutes substantial C_{inorg} carbon stocks estimated between 11 and 39 Tg C_{inorg} (Mazarrasa *et al*., 2015). Thus, understanding the amount and the source of carbonates in seagrass ecosystems is crucial to determine their role as carbon sink or carbon source (Mazarrasa *et al*., 2015; Macreadie *et al*., 2017; Gullström *et al*., 2018; Saderne *et al*., 2019).

In the Mediterranean Sea, the endemic seagrass species *Posidonia oceanica* (Linnaeus) Delile constitutes extensive meadows considered as a unique carbon sink due to the development of an outstanding structure known as “matte” (Molinier and Picard, 1952). This complex belowground formation, composed of intertwined rhizomes, roots and leaf sheaths embedded in the sediment, exhibits a very low decay rate in relation with the highly refractory nature of the organic matter and the anoxic conditions (Romero *et al*., 1992; Mateo *et al*., 1997, 2006; Kaal *et al*., 2018). The accretion of organic material in coastal sediments beneath the *P. oceanica* meadows constitutes one of the largest carbon sinks in coastal areas worldwide and can reach several meters in height and remain over millennia (Lo Iacono *et al*., 2008; Serrano *et *al*., 2012). The global importance of *P. oceanica* meadows as a long-term carbon sink has been widely recognized due to their formation of large carbon stocks and their extensive distribution in the Mediterranean Sea (Romero *et al*., 1994; Mateo *et al*., 1997, 2006; Serrano *et al*., 2012, 2014, 2016a).

The estimates of carbon stocks beneath *P. oceanica* seagrass meadows have been based on the analysis of a large number of sediment cores allowing characterization of the potential variability of sedimentary carbon stocks and fluxes (Mateo *et al*., 1997; Lo Iacono *et al*., 2008; Serrano *et al*., 2012, 2014, 2016a; Mazarrasa *et al*., 2017; Apostolaki *et al*., 2019; Piñeiro-Juncal *et al*., 2021; Wesselmann *et al*., 2021). The works performed in the last decade have emphasized the need to improve the global estimates of carbon stocks and fluxes (i) by increasing the number of direct measurements in seagrass sediments, and (ii) by accounting for biogeochemical factors driving variability within habitats (Pergent *et al*., 2012, 2014; Mazarrasa *et al*., 2018). For this purpose, the current study aimed (i) to understand the spatial variability in the C_{org} and C_{inorg} stocks in the matte of a *P. oceanica* meadow located on the eastern coast of Corsica Island, and (ii) to provide a global estimate of the C_{org} and C_{inorg} stored at regional scale.

2. Material and methods

2.1. Study site

This study was conducted on the eastern continental shelf of Corsica Island (France, NW Mediterranean Sea; Fig. 1.a; Fig. 1.b). This extensive geographical area was selected because it presents a wide range of environmental conditions (Appendix S1).

The study was mainly conducted in the Natura 2000 area, “FR9402014 - Grand Herbier de la Côte Orientale”, located between the mouth of the Biguglia lagoon in the north and the mouth of the Solenzara river in the south (Meinesz *et al.*, 1990). The site stretches along 106 km sandy coast and is characterized by the presence of multiple lagoons (*e.g.* Biguglia, Diana, Urbino, Palo) and by freshwater inputs from the main coastal rivers of Corsica (*e.g.* Golo, Tavignano, Travo; Cannac-Padovani *et al.*, 2014). This site hosts one of the largest *P. oceanica* meadows in the Mediterranean Sea, covering a surface area of 20 425 ha (Fig. 1.c), which represents 52% of the sea bottom between 0 and 50 m depth (Valette-Sansevin *et al.*, 2019). This continuous meadow grows on a sandy substrate and is influenced by local high-energy hydrodynamic currents as suggested by the presence of frequent intermattes (Clabaut *et al.*, 2010; Abadie *et al.*, 2015).

Other investigations were performed between the mouth of the Solenzara in the north and the gulf of Porto-Vecchio in the south (Fig. 1.c). This area covers a 25 km stretch of rocky coast and is constituted by a succession of small beaches and bays. The irregular topography of the sea bottom is mainly dominated by hard substrate with infralittoral photophilous algae and *P. oceanica* seagrass meadows. The influence of nearshore high exposure to hydrodynamic energy and wave action in the *P. oceanica* meadow was evidenced by the presence of erosive structures such as ‘return rivers’ (*i.e.* sand channels perpendicular to the coast; Boudouresque *et al.*, 2012) and the presence of meadows from 10 m depth (Vacchi *et al.*, 2016). In contrast to the sandy coast where the lower limit of the *P. oceanica* meadows can be observed at distances of more than 8 km from the shoreline, the geomorphology and the slope of the continental shelf limited the meadow extension towards the open ocean (<1 km; Valette-Sansevin *et al.*, 2019).

2.2. Sampling in *Posidonia oceanica* meadows

The sediment sampling was performed in 2018 during the oceanographic research survey Carbonsink aboard the R/V 'L'Europe' (Ifremer). The collection of the cores was undertaken after the acquisition and processing of acoustic and seismic reflection data enabled production of a continuous map of marine benthic habitats and an estimation of matte thickness on the eastern coast of Corsica Island (Valette-Sansevin et al., 2019; Monnier *et al.*, 2020a, 2020b, 2021b). In total, 48 cores were sampled at 12 locations and 22 stations (Fig. 1.c; Appendix S1; Appendix S2). At each station, one to three replicates were sampled (α, β and γ) ca. 50 m from each other. On the sandy coastline, the cores were mainly collected between 10 and 40 meters depth along three transects at Biguglia (BG), Taverna (TV) and Urbino (UB) (Fig. 1.d; Fig. 1.e; Fig. 1.f; Appendix S1). Across the study area, additional cores were also sampled at specific stations: Arinella (AR), Marana lido (ML), Golo river mouth (GM), Golo river delta (GD), Tavignano river mouth (TM) and Solenzara river mouth (SM). Additionally, three cores, equidistantly distributed along the rocky coastline, were sampled at Canella (CN), Fautea (FT) and Saint-Cyprien (SC) (Fig. 1.c; Fig. 1.g). The sediment sampling was achieved using a Kullenberg gravity corer. The corer barrel consisted of a stainless-steel tube 3 to 5 meters long with a PVC tube (internal diameter 90 mm) inside it and surmounted by a lead weight of approximately 700 kg. Compression of unconsolidated sediment during coring is an inevitable phenomenon. In order to minimize this effect, the core head was constituted by a sharp edge to cut the fibrous material of the matte. Corrections were applied to decompress the sediment sequence by distributing the spatial discordances proportionally to the expected and the observed soil column layers (Glew *et al.*, 2001; Howard *et al.*, 2014a). For the different cores, the average compression was estimated at between 10% and 20% and the corrected core lengths ranging from 40 to 380 cm (Appendix S2).

For the elemental and isotopic composition analysis of the main allochthonous or autochthonous potential carbon sources contributing to the carbon sink, (*i.e. P. oceanica* shoots, macroalgae and epiphytes) were manually collected by SCUBA diving at each station of the Taverna (TV) transect. For each station, the macrophytes sampling was undertaken in three quadrats of 20 cm x 20 cm randomly distributed in a 5 m radius area around the coring station. In addition, 10 liters of seawater were collected from 2 m above the sea bottom (GM, BG, TV, TM, and UB stations) with Niskin bottle (General Oceanics, Miami, USA) and filtered into prewashed and precombusted (450°C, 3 h) Whatman GF/F 47 mm filters directly after collection for SPOM elemental and isotopic analysis. All the samples were refrigerated at 2°C until analysis in the laboratory.

2.3. Laboratory analyses

All cores collected were subsampled on the research vessel according to two strategies. The first strategy consisted in subsampling sediment cores (1 cm-thick slices every 5 cm) in order to obtain a detailed and regular pattern of biogeochemical parameters in the matte. This subsampling approach was applied to cores with the deepest matte profiles at each station (Appendix S2). The second strategy involved the subsampling of sediment cores at irregular intervals with higher subsampling effort in the top 50 cm where variations in C_{org} content are most significant (1 cm-thick slices every 5-10 cm in the top 50 cm of cores and every 20-25 cm over the rest of the core; Howard *et al.*, 2014a; Mateo *et al.*, 2019). This second subsampling strategy was applied to replicate cores taken within the same station allowing the collection of subsequent information within a station and the study of the variability in C_{org} and C_{inorg} content in the matte. Bulk density (g DW cm^{-3}) was measured after drying samples at 70°C until constant weight (Howard *et al.*, 2014a). Each sample was disaggregated manually with a spatula, sieved through a 2 mm-mesh sieve and then separated into two fractions: fine (<2 mm) and coarse (>2 mm). The fine fraction was composed of the inorganic and organic matter of the sediment (SOM). The coarse fraction was sorted into 3 different categories: (i) the coarse organic fraction (COM, fragments of *P. oceanica*), (ii) the coarse mineral fraction (gravel), and (iii) the coarse calcium carbonate fraction (shells and biogenic debris; $CaCO_3$ >2 mm). After the sorting step, the COM was integrated with the fine fraction, ground, and homogenized for further analysis (Monnier *et al*., 2020a).

The total organic matter (TOM) and calcium carbonate content ($CaCO_3$ <2 mm) in sediment samples (ca. 3 g aliquots) were determined by the method of loss on ignition at 550°C for 5 h (LOI_{500}) and 950°C for 2 h (LOI_{950}) in a muffle furnace (Heiri *et al*., 2001). Each LOI analysis (batch of n = 18 samples) was performed with reference samples of seagrass sediment (POSIDTAV; LOI_{550}: 8.07 ± 0.25% TOM; n = 60) and pure $CaCO_3$ (Merck EMSURE®, Darmstadt, Germany) in order to correct any incomplete combustion of sediment samples. The average correction factors for LOI_{550} and LOI_{950} were estimated at 1.00 ± 0.03 and 1.02 ± 0.02, respectively. The TOM content represents the total amount of SOM (<2 mm) and COM (>2 mm) and the total $CaCO_3$ content corresponds to the total amount of $CaCO_3$ <2 mm and >2 mm. The total content in inorganic carbon ($\%C_{inorg}$) was calculated through stoichiometry using the mass of carbon (A_r= 12) and the molecular weight of $CaCO_3$ (M_r = 100) according to Rozaimi *et al*. (2016). Another aliquot of ground sub-samples (ca. 1 g) was used for elemental composition ($\%C_{org}$) and isotopic analyses ($\delta^{13}C$) by firstly acidifying them with hydrochloric acid (HCl 1M) to remove all $CaCO_3$. After cessation of effervescence, the sediment was centrifuged (3500 RPM, 2-3 min), rinsed with deionized (MilliQ™) and the supernatant with acid residues removed using a pipette. Deionized water was added to wash off the residual acid, centrifuged again and the supernatant removed until pH = 7. The residual samples were re-dried (70°C), weighted and placed in tin capsules (10-20 mg).

The elemental and isotopic composition was also analyzed in belowground (sheaths, rhizomes, and roots) and detrital samples (litter) of *P. oceanica*, epiphytes, macroalgae (*Padina pavonica*, *Peysonnellia squamaria Flabellia petiolata*, *Codium bursa*, *Dictyota dichotoma*, *Osmundaria volubilis*, *Rythiphlaea tinctoria*) and SPOM. The epiphytes were collected from the living leaves of *P. oceanica* shoots following the method of Alcoverro et al. (1997). The epiphytes and belowground organs of seagrass were pooled in two groups for analysis. The macrophytes and epiphytes were successively cleaned in deionized water, decarbonated following acidification with HCl 0.1N, re-rinsed with deionized water and finally dried at 70°C. The filters in which SPOM was collected were dried to constant weight and fumed under concentrated HCl fumes (2M) overnight at room temperature in glass desiccator and under vacuum. After decarbonation, plant samples and filters were also placed in tin capsules.

Measurements of C_{org} elemental composition and stable isotope ratios were performed using an elemental analyzer EA2000 (Thermo Scientific, Milan, Italy) coupled to a continuous-flow isotope-ratio mass spectrometer (IRMS) analyzer Delta V Advantage (Thermo Scientific, Bremen, Germany) through a Conflo IV interface (Thermo Scientific, Milan, Italy) at the LIENSs Stable Isotope Facility (UMR CNRS 7266, University of La Rochelle, France). The certified standard samples used during analyses were USGS-61 (Caffeine; %C: 49.40 ± 0.38%; $\delta^{13}C$: -35.05 ± 0.04‰) and USGS-62 (Caffeine; %C: 49.42 ± 0.35%; $\delta^{13}C$: -14.79 ± 0.04‰) (USGS, Reston Stable Isotope Laboratory; Schimmelmann *et al.*, 2016). The analytical precision of the elemental (%C) and isotopic ($\delta^{13}C$) measurements based on the standard deviation of replicates of the standards was <0.3 % and <0.05‰, respectively. Carbon isotope ratios are expressed as δ values in parts per thousand (‰) relative to VPDV (Vienna Pee Dee Belemnite) according to standard notation ($\delta^{13}C = [(R_{sample} / R_{standard}) - 1] \times 10^3$, where R is the ratio $^{13}C/^{12}C$).

2.4. Numerical procedures

The analysis of C_{org} content was performed in a limited number of samples (7 to 25) for regularly subsampled cores. The C_{org} content in the remaining samples was inferred using the equation obtained from the linear regression existing between TOM (%DW) and C_{org} (%DW) contents measured in the same sample for each core. For irregularly subsampled cores where elemental analysis was not assessed, the C_{org} content was determined using the relationship between %TOM and %C_{org} equation obtained for the nearest regularly subsampled cores (*i.e.* same station). The C_{org} content was referred to the initial bulk sediment weight (*i.e.* pre-sieved and pre-acidified) and expressed as a percentage (%).

The organic and inorganic carbon density in each sample was calculated by multiplying the sediment dry bulk density (g cm^{-3}) by the organic or inorganic carbon content (%C_{org} or %C_{inorg}) to obtain the carbon density (g C_{org} cm^{-3} or g C_{inorg} cm^{-3}). The carbon density was multiplied by the sediment thickness considered to obtain the stock in the sample per unit area (g C_{org} cm^{-2} or g C_{inorg} cm^{-2}). The cumulative C_{org} and C_{inorg} stock per core was computed by adding the value of all samples and normalized to stratigraphic depths of 100 cm and 250 thick deposits to allow comparisons. The limit of 100 cm was used to compare values with other studies. The C_{org} and C_{inorg} stocks for 250 cm matte thickness (*i.e.* mean thickness; Monnier *et al.*, 2021b) were inferred for the remaining cores by using linear regression.

Statistical analyses were performed using the statistics software package XLSTAT (Addinsoft, 2019) for Microsoft Office Excel® 2016. Normality of parameter values was checked using a Shapiro-Wilk test. Any differences among sites, depth, matrix (*i.e.* sand matrix/rock matrix) and depositional environment in bulk density, TOM and $CaCO_3$ content, C_{org} and C_{inorg} content (%), $\delta^{13}C$ (‰), and carbon stocks (kg C_{org} m^{-2} and kg C_{inorg} m^{-2}) were analyzed using one-way Analysis of Variance (ANOVA). When significant effects were detected by ANOVA, pairwise *a posteriori* comparisons were performed using Tukey's honest significant difference (HSD) tests. When necessary, data were log transformed to meet ANOVA assumptions. The relationships between the variables and the environmental parameters were analyzed using the Pearson correlation coefficient. The correlation coefficient was calculated together with p-values to determine the significance and strength of each relationship. When necessary, the data were log transformed to improve linearity.

In the study site, the estimates of C_{org} and C_{inorg} stored in the matte of *P. oceanica* meadows were performed using multibeam echosounder (MBES) data compiled in a morpho-bathymetric Digital Terrain Model (DTM) raster mosaic with a spatial resolution of 10 x 10 m and a vertical accuracy of 0.2 m (Monnier *et al.*, 2020a). The DTM was integrated (Mercator projection - WGS 1984) in a Geographic Information System (GIS) software (ArcGIS® 10.0; ESRI, 2011). Benthic habitat mapping of the sea bottom was used to select the surface occupied by the *P. oceanica* meadows at the study site (Valette-Sansevin *et al.*, 2019). The C_{org} and C_{inorg} stock was estimated to the normalized depth of 100 cm and 250 cm (see above). The mean values collected at the different depths (10 m to 40 m depth) were used to fit linear regression equations. The continuous predictive maps of C_{org} and C_{inorg} stocks within the study site were produced by integrating the linear regression formulae in the sea bottom DTM ('Raster Calculator' tool; ArcGIS® 10.0; ESRI, 2011). The regional estimates (Corsica) were based on the surface areas occupied by *P. oceanica* meadows along the coastline (53 735 ha; Valette-Sansevin *et al*., 2019) and the mean stocks found at the study site.

In order to assess the contribution of long-term carbon sinks to climate change mitigation, the annual CO_2 release at regional scale (Corsica) was calculated by multiplying the CO_2 release per capita in France in 2018 (5.2 t CO_2 yr^{-1} $capita^{-1}$; Gilfillan *et al*., 2019; UNFCCC, 2019; BP, 2019) and the population estimated for Corsica (Pergent-Martini *et al*., 2020). For this assessment, the carbon stock values calculated in this study were converted into CO_2 equivalent (CO_{2e}) multiplying by 3.67 (Howard *et al*., 2014a). The net CO_{2e} stock (*i.e.,* balance between C_{org} stock (CO_2 sink) and the C_{inorg} stock (CO_2 source)) was estimated in different environmental conditions considering the CO_2 emission occurring during calcification process ('rule of the 0.6'; Ware *et al*., 1992; Frankignoulle *et al*., 1994). The net CO_{2e} stock assessment was estimated by subtracting CO_2 emitted from the C_{org} stocks through the method established in Howard *et al*. (2014b) and Macreadie *et al*. (2017) by following this equation:

$$\text{net } CO_{2e} \text{ stock} = [\, C_{org} \text{ stock} - \psi \times C_{inorg} \text{ stock} \,] \times 3.67 \qquad \text{(Eq. 1)}$$

where C_{org} and C_{inorg} stock are the C_{org} and C_{inorg} stored (in kg C_{org} m^{-2} and kg C_{inorg} m^{-2}, respectively) and ψ is the gas exchange : reaction ratio of CO_2 and $CaCO_3$ proposed by Smith (2013) (ψ = 0.6, estimated for the shallow waters and used by Mazarrasa *et al*., 2015). The equation was applied assuming that all soil carbon stocks in the *P. oceanica* meadows resulted from autochthonous sources (no export of autochthonous carbon and no import of allochthonous carbon) as reported by Howard *et al*. (2014b). Upscaling of the net CO_{2e} stock within the study was undertaken using Eq. 1 and predictive maps of C_{org} and C_{inorg} (see above) through a spatial analysis ('Raster Calculator' tool; ArcGIS® 10.0; ESRI, 2011) to emphasize the areas acting as CO_2 sink or source.

3. Results

3.1. Biogeosedimentological characterization of the matte

Among the 48 cores collected on the eastern continental shelf of Corsica, 39 were mainly constituted by seagrass plant remains (sheaths, rhizomes, and roots) incorporated into a dark brown sandy-muddy sedimentary matrix. The material analysis has enabled identification of extensive well-preserved seagrass organic debris buried down to the deepest parts of sediment (>350 cm). The biogeosedimentological features of the *P. oceanica* matte changed substantially with stratigraphy (*i.e.* level in the soil; Table 1), environmental parameters (*i.e.* depth, sediment matrix, and depositional environment; Fig. 2; Appendix S3) and across the site (Appendix S3).

Considering the first meter of cores, the bulk density ranged from 0.15 to 1.91 g DW cm^{-3} with an average value (± S.E.) of 1.07 ± 0.02 g DW cm^{-3} (Fig. 2.a; Appendix S3). Bulk density showed significant differences between stations (one-way ANOVA, $p<0.0001$) and increased with level in the sediment from 0.67 ± 0.07 to 1.23 ± 0.08 g DW cm^{-3} ($r = 0.575$; $p<0.001$; Table 1). However, bulk density showed no relation with depth, sediment matrix, and depositional environment (Fig. 2.a).

The average composition of matte cores was characterized by a high content in organic matter (7.62 ± 0.25 %TOM in the top 100 cm of matte; Fig. 2.b) declining with level in the soil ($r = -0.418$; $p<0.001$; Table 1). The highest and lowest %TOM were observed at Golo mouth (GM-10;

11.13 ± 0.75 %) and Taverna transect (TV-30; 2.50 ± 0.38 %; Appendix S3). The shallow stations (10-20 m) exhibited an approximately two-fold higher content in TOM than deeper ones (30-40 m), with respectively 8.22 ± 0.54 % and 4.19 ± 0.54 % (Fig. 2.b). Furthermore, seagrass meadows located near estuary areas had significantly higher %TOM than coastal ones ($p<0.01$; Fig. 2.b).

Organic carbon content (%C_{org}) over the first 100 cm of matte ranged between 0.88 and 23.27 % (mean: 3.67 ± 0.12 %) with highest values recorded at Golo mouth (5.27 ± 0.26 %; Fig. 2.c; Fig A.1.c). Similarly to %TOM, significant decreases in %C_{org} were observed with level in the matte ($r = -0.364$; $p<0.001$; Table 1) and depth ($p<0.0001$; Fig. 2.c). However, although no significant difference was observed with depositional environment, the matte surrounded by rocky substrate (2.16 ± 0.32 %) showed lower %C_{org} compared to *P. oceanica* meadows growing on sandy substrate (3.74 ± 0.12 %; $p<0.0001$; Fig. 2.c).

The contribution of the OM sources in the sediment was calculated in the first meter of matte over 11 stations and varied significantly with site, depth, level in the soil, and the depositional environment ($p<0.0001$; Fig. 2.d; Table 1). The $\delta^{13}C$ isotopic signature found in the organic fraction of the matte ranged between -9.69 to -20.91 ‰ with an average value of -16.21 ± 0.31 ‰ (Fig. 2.d). Values increased between the surface layers (-18.13 ± 0.47 ‰) to the bottom end of the section (-14.55 ± 1.60 ‰; $r = 0.285$; $p<0.001$; Table 1; Fig. 2.d; Appendix S3). Matte located in shallow and estuarine areas was significantly more depleted in ^{13}C compared to deep and coastal areas ($p<0.0001$; Table 1; Fig. 2.d; Fig. 3.b). Sandy and rocky locations showed homogenous values with -18.03 ± 0.02 ‰ and -18.66 ± 0.22 ‰ (Fig. 3.b).

Among the potential carbon sources, *P. oceanica* combined tissues showed the most ^{13}C-enriched values (-10.94 to -14.31 ‰; mean: -12.49 ± 1.27 ‰; Fig. 3.a), while SPOM had the most

^{13}C-depleted values (-20.26 to -24.28 ‰; mean: -23.09 ± 0.91 ‰). Macroalgae sources exhibited greater variability (from -12.43 ‰ for *Codium bursa* to -28.01 ‰ for *Flabellia petiolata*), with an average estimated value of -18.69 ± 5.11 ‰ (Fig. 3.a). Autochthonous sources (*P. oceanica* tissues) showed a high contribution to the sedimentary stock notably in the lower section of the matte (30-100 cm; r = 0.285; p<0.001), deep stations (r = 0.660; p<0.001) with reduced influence of estuarine environment (p<0.0001; Table 1; Fig. 3.a; Fig. 3.b).

The composition of the matte exhibited a high content in calcium carbonate (%$CaCO_3$) and inorganic carbon (%C_{inorg}; Fig. 2.e; Fig. 2.f). Over the first 100 cm, the $CaCO_3$ fraction was two- to three-fold higher than %TOM representing on average 18.86 ± 0.85 % and reaching up to 59.04 ± 0.85 % (Appendix S3). The C_{inorg} content of the matte accounted for 2.25 ± 0.10 % and was estimated at between 0.35 and 7.08 % (Appendix S3). The highest and lowest $CaCO_3$ and C_{inorg} content were recorded for the Golo delta station (GD-40; 47.71 ± 2.67 %$CaCO_3$ and 5.67 ± 0.36 %C_{inorg}) and for the shallowest location in Urbino transect (UB-10; 4.57 ± 0.32 %$CaCO_3$ and 0.55 ± 0.04 %C_{inorg}). A significant increase was observed from shallow stations (13.46 ± 0.95 %$CaCO_3$ and 1.62 ± 0.11 %C_{inorg}) to deep stations (31.96 ± 2.38 %$CaCO_3$ and 3.77 ± 0.28 %C_{inorg}; p<0.0001; Fig. 2.e; Fig. 2.f; Table 1). Furthermore, rocky and coastal stations proved to have a significantly higher %$CaCO_3$ and %C_{inorg} than sandy and estuary stations (<0.0001; Fig. 2.e; Fig. 2.f).

3.3. C_{org} and C_{inorg} stocks

The mean standing C_{org} and C_{inorg} stocks per unit area show a significant variability between stations (p<0.0001; Fig. 4; Appendix S4). For 100 cm- and 250 cm-thick matte, the highest C_{org} stocks were recorded at BG-10 with 44.3 kg m^{-2} and 111.3 kg C_{org} m^{-2}, respectively

(Appendix S4). The C_{org} stock, estimated on average at 32.7 ± 1.5 kg C_{org} m^{-2} in the first 100 cm (Appendix S4), reached 72.3 ± 4.6 kg C_{org} m^{-2} for the first 250 cm (Appendix S4). The C_{inorg} stock occurring in *P. oceanica* matte deposits accounted for an important part of the total carbon stock, exceeding the C_{org} stock at some stations (Appendix S4). The mean stocks were estimated at 24.5 ± 4.5 kg C_{inorg} m^{-2} and 60.5 ± 9.9 kg C_{inorg} m^{-2} for 100 cm- and 250 cm-thick matte deposits. The maximum C_{inorg} stocks were reported at BG-30 for 100 cm- (72.4 kg C_{inorg} m^{-2}) and 250 cm-thick matte deposit (160.1 kg C_{inorg} m^{-2}; Appendix S4).

Whatever the soil level considered, the C_{org} and C_{inorg} stocks in the *P. oceanica* matte varied significantly with depth, sediment matrix and depositional environment (p<0.0001; Fig. 4). The C_{org} stocks decreased through depth (p<0.0001; Fig. 4.a, Fig. 4.c) from 35.8 ± 1.3 to 26.1 ± 1.1 kg m^{-2} (100 cm-thick deposits) and from 87.2 ± 4.9 to 39.5 ± 3.2 kg m^{-2} (250 cm-thick deposits). In contrast, deep meadows stored significantly more C_{inorg} in the matte compared to shallow meadows (p<0.0001; Fig. 4.b; Fig. 4.d). The C_{inorg} stock ranged from 18.6 ± 4.4 and 44.7 ± 3.7 kg m^{-2} (100 cm) and from 48.1 ± 9.4 to 102.6 ± 0.2 kg m^{-2} (250 cm). The matte of seagrass meadows growing on sandy substrate showed substantially higher C_{org} stocks than those on rocky substrate (p<0.0001; Fig. 4.a, Fig. 4.c). In contrast to rocky matrix, the C_{inorg} stock occurring in the matte of seagrass meadows growing on sandy substrate differed substantially with the soil level (p<0.0001; Fig. 4.b; Fig. 4.d). The C_{inorg} stocks in sandy areas increased exponentially within soil depth (3.5-fold from 100 cm to 250 cm) compared to rocky areas (1.3-fold). Also, between depositional environments, the C_{org} stocks occurring in seagrass soils were homogenous (Fig. 4.a; Fig.4.c). Inversely, coastal meadows displayed approximately 1.5- to 2.0-fold higher C_{inorg} stocks than estuarine ones (p<0.0001; Fig. 4.b; Fig.4.d).

3.4. Estimates of C_{org} and C_{inorg} stocks

The estimates of C_{org} and C_{inorg} stocks associated with *P. oceanica* meadows on the eastern coast of Corsica Island were based on the relationship between the carbon stocks and depth gradient observed in this study (Fig. 4). Thus, the mean C_{org} and C_{inorg} stock values determined in the top 100 cm and 250 cm of *P. oceanica* matte coupled to the corresponding depth were used to fit linear regression curves (Appendix S5). The C_{org} stock-depth relationships were negatively correlated whereas C_{inorg} stock-depth were positively correlated (Appendix S5). Upscaling of C_{org} and C_{inorg} stocks was undertaken after integrating the respective functions describing the variation in stocks with depth into the morpho-bathymetric DTM raster mosaic of the sea bottom (Appendix S6). The mean stocks in the first meter of matte were estimated at 32.0 ± 0.2 kg C_{org} m^{-2} and 28.7 ± 0.1 kg C_{inorg} m^{-2} (Appendix S6). At the study site, the total amount of carbon stored reached 6.5 million t C_{org} and 5.9 million t C_{inorg}. Considering the top 250 cm of matte, the carbon stocks were estimated at 68.7 ± 0.1 kg C_{org} m^{-2} and 69.2 ± 0.1 kg C_{inorg} m^{-2} (Appendix S6). The overall quantity of carbon stored in the mean thickness of matte (250 cm) was assessed at 28.2 million t (14.0 million t C_{org} and 14.2 million t C_{inorg}).

The net CO_2 stocks have been estimated for the first 100 cm and 250 cm matte deposits of the *P. oceanica* meadow according to water depth, substrate, and depositional environment (Table 2). Except the deep bathymetric range (between 30 m and 40 m depth), *P. oceanica* meadows along the eastern coast of Corsica appeared to constitute net CO_2 sinks. The contribution of the top 100 cm (Fig. 5.a) and the top 250 cm of *P. oceanica* matte (Fig. 5.b) as carbon sink or carbon source have been modeled through the use of the morpho-bathymetric DTM raster mosaic of the sea bottom. The surface areas considered as CO_2 sources have been assessed at 561.7 ha (100 cm; Fig. 5.a) and 3 960.2 ha (250 cm; Fig. 5.b) which represents 2.8% and 19.4% of the total surface area occupied by seagrass meadows at the study site.

4. Discussion

4.1. Variability in C_{org} stocks

The present study showed a significant variability in the C_{org} stored in the sedimentary compartment found beneath *P. oceanica* meadows. At site scale, the C_{org} stocks in the first meter of *P. oceanica* sediment (14.4-44.3 kg C_{org} m^{-2}) were consistent with other values determined throughout the Mediterranean Sea (4.7-75.5 kg C_{org} m^{-2}; Romero *et al*., 1994; Mateo *et al*., 1997, 2006; Serrano *et al*., 2012, 2014, 2016a; Piñeiro-Juncal *et al*., 2021). These values confirm that C_{org} stock per unit area in the *P. oceanica* matte deposits is an exception in seagrass ecosystems (Lavery *et al*., 2013; Rozaimi, 2015) and one of the highest ever recorded in coastal and marine ecosystems (Laffoley and Grimsditch, 2009; Mcleod *et al*., 2011; Duarte *et al*., 2013; Alongi, 2018).

The stocks of C_{org} accumulated in sediments of *P. oceanica* and *Posidonia* spp. decreased with depth (Serrano *et al*., 2014, 2016a; 2016b). Here, the two- to three-fold difference observed in C_{org} accumulation with depth gradient (10 m and 20 m depth) confirms this trend in the first 100 cm of sediment. Even though previous studies demonstrated significant reduction in C_{org} accumulation rates and stocks in the upper section (20 cm) of *P. oceanica* sediments along depth gradients (Romero *et al*., 1992; Mateo and Romero, 1997), here no significant change in C_{org} stock of shallow sediments (30 cm) was observed with depth. Inversely, the C_{org} stored in the top 100 cm and 250 cm of matte deposits exhibited a two- to three-fold difference between 10 m and 40 m depth confirming the significant influence of depth in the storage of C_{org} in seagrass soils (Mateo and Romero, 1997; Serrano *et al*., 2014, 2016a; Samper-Villareal *et al*., 2016).

Mapping of benthic habitats undertaken along the Corsican shoreline demonstrated that the depth distribution of seagrass meadows at site level is very extensive (Valette-Sansevin *et al.*, 2019) and corresponds to the depth range reported throughout the Mediterranean (Duarte, 1991; Boudouresque et al., 2012). Although *P. oceanica* meadows occupy areas down to 40 m water depth, light reduction associated with depth gradient has a significant effect on the plant primary production and canopy complexity which are key determinant factors influencing both the C_{org} sequestration and storage capacity of seagrass meadows (Alcoverro *et al.*, 2001; Collier *et al.*, 2007; Serrano *et al.*, 2014). Thus, an increase in seagrass canopy complexity (*i.e.* density, cover and biomass) contributed generally to the reduction of hydrodynamic energy resulting in higher trapping and retention of fine-grained sediment particles (*i.e.* silt and clay) from the water column, and consequently leading to higher sediment accretion rates (SAR) (Gacia and Duarte, 2001; Hendriks *et al.*, 2008; Samper-Villarreal *et al.*, 2016; Serrano *et al.*, 2016b; Monnier et al., 2021b). Concurrently, the higher deposition of fine sediment particles and SAR of seagrass soils may contribute to an increase in C_{org} burial rates and preservation (Keil and Hedges, 1993; Burdige, 2007) due to reduced oxygen exposure time occurring in fine sediments (Hedges and Keil, 1995; Mateo *et al.*, 2006; Burdige, 2007; Pedersen *et al.*, 2011). Recently, the *P. oceanica* primary production and C_{org} sequestration along depth-related gradients were assessed within the study area (Pergent-Martini *et al.*, 2020). The overall decrease in the canopy complexity (shoot density) and productivity (mean total C_{org} capture and sequestration) observed in the 5-30 m depth range coincides with our results revealing a decline in C_{org} stocks with depth.

Similar to the effects initiated by water depth, the increased turbidity resulting from terrestrial inputs in estuarine environments was expected to affect the C_{org} stocks in *P. oceanica* seagrass sediments within the study area. Light attenuation has been confirmed to decrease meadow productivity and canopy complexity (Alcoverro *et al.*, 2001; Ruiz and Romero, 2001; Collier *et al.*, 2009) contributing to lower sequestration of autochthonous C_{org} (Keil and Hedges, 1993; Gacia and Duarte, 2001; Burdige, 2007). However, no significant difference was established between the sedimentary C_{org} stocks found within sediments of the two depositional environments. Consequently, the deposition of fine-grained sediment particles likely contributes to preserve autochthonous C_{org} after burial and reduce remineralization of organic compounds related to reduced oxygen concentrations in fine sediments (Keil and Hedges, 1993; Mateo *et al.*, 2006; Burdige, 2007). This hypothesis seems to be confirmed by the lower isotopic signature of seagrass sediments organic matter in Golo and Tavignano estuarine environments (Appendix S3), suggesting a higher deposition of allochthonous particles at these sites which may increase the C_{org} preservation efficiency. Higher deposition of C_{org} allochthonous particles from terrestrial- or sestonic inputs may also offset the reduction in autochthonous inputs due to light attenuation resulting in comparable C_{org} stocks in seagrass deposits (Samper-Villareal *et al.*, 2016; Ricart *et al.*, 2020).

Although *P. oceanica* meadows has been described in historical literature as a species growing mainly on soft nutrient-rich substrates (Molinier and Picard, 1952), the species also colonizes rocky substrates following the development of algal turf assemblages or penetration of roots through crevices (Pérès and Picard, 1964; De Falco *et al.*, 2003, 2008; Boudouresque *et al.*, 2012). The *P. oceanica* meadows growing on rocky substrate are usually influenced by higher exposure to hydrodynamic energy and lower particle deposition compared to sheltered areas (Fonseca and Bell, 1998; Vacchi *et al.*, 2017a). In comparison with sheltered areas, the growth of exposed meadows (*i.e.* on rocky substrate) tends to be horizontally-oriented resulting in the development of a thinner matte (<1 m; De Falco *et al.*, 2008; Vacchi *et al.*, 2017a). In response to lower sediment deposition, meadows on rocky matrix exhibited a lower shoot density than on sandy substrate for comparable depths, a higher proportion of plagiotropic shoots than sheltered meadows but a lower orthotropic rhizome growth rate, as shown in Sardinia and Sicily (De Falco *et al*., 2008; Di Maida *et al.*, 2013). By influencing the deposition of allochthonous particles in exposed seagrass meadows, marine currents and waves may affect the C_{org} accumulation and storage in seagrass meadows (Samper-Villareal *et al.*, 2016; Mazarrasa *et al*., 2017, 2018). Here, seagrass sediments at sandy sites showed two-fold higher C_{org} stocks compared to rocky areas, whatever the thickness of matte considered. This difference may be explained by the lower content of fine sediment particles found in exposed areas, the erosional patterns, and the high remineralization rates of already buried C_{org} in seagrass sediments found on rocky matrix, likely related to hydrodynamic processes enhancing oxygen diffusion through the sediment (Gacia *et al*., 2002; Burdige, 2007; Samper-Villareal *et al*., 2016; Serrano *et al.*, 2016b, 2016c).

4.2. Variability in organic matter sources

The changes in $\delta^{13}C$ signature (Fig. 3.a) confirmed that both seagrass-derived (autochthonous sources) and non-seagrass-derived materials (allochthonous sources) were preserved in *P. oceanica* meadow sediments (Gacia *et al*., 2002; Kennedy *et al*., 2010). In this study, the seagrass-derived OM was shown to be more enriched in ^{13}C (-12.49 ± 1.27 ‰) compared to algal- and sestonic-derived OM (-18.69 ± 5.11 ‰ and -23.09 ± 0.91 ‰, respectively; Fig. 3.b) as reported by Kennedy *et al*. (2010). The isotopic signature of *P. oceanica* seagrass materials described in this study was shown to be consistent with values observed in previous studies (-13.9 ± 1.0 ‰ to -11.9 ± 4.1 ‰; Hemminga and Mateo, 1996; Lepoint *et al*., 2000; Gacia *et al*., 2002; Kennedy *et al*., 2010). As in many other meadows, the $\delta^{13}C$ signature of *P. oceanica* seagrass sediments measured in the first meter of soil showed lower values relative to the seagrass tissues (Kennedy *et al*., 2010), likely due to a contribution of different carbon sources to the C_{org} accumulated in seagrass sediments (Kennedy *et al*., 2004; Papadimitriou *et al.*, 2005).

Over the first meter of sediment, $\delta^{13}C$ values increased continuously from the surface to the bottom end of the section (-18.13 ± 0.47 ‰ to -14.55 ± 1.60 ‰). These differences in $\delta^{13}C$ values probably result from the different decomposition rates of the different OM sources accumulated within the sediment layers. In contrast to high-biomass and persistent seagrass species such as *P. oceanica* containing relatively high amounts of refractory organic compounds (*e.g.* lignin, cellulose) which delays their mineralization (Duarte and Chiscano, 1999; Klap *et al*., 2000; Pedersen *et al*., 2011; Kaal *et al*., 2016, 2018), allochthonous organic matter sources deriving particularly from macroalgae and sestonic sources are richer in labile C_{org} compounds leading to early decomposition during diagenesis (Enriquez *et al*., 1993; Mateo and Romero, 1997; Klap *et al*., 2000; Cebrian *et al.*, 2002; Gacia *et al*., 2002). Consequently, the shifts in $\delta^{13}C$ values over the first meter of matte suggest that C_{org} from persistent seagrass-derived materials (*e.g.* rhizomes) are more preserved in sediments and exhibited no major change over time in contrast to labile forms of C_{org} associated with algal and sestonic sources which are more vulnerable to remineralization (Henrichs, 1992, Enriquez *et al*., 1993; Burdige, 2007; Serrano *et al*., 2016b, 2016c).

Likewise, the significant changes of $\delta^{13}C$ values observed in the first meter of matte deposits along a water depth gradient and depositional environment confirm that abiotic factors influence contribution of allochthonous OM to the long-term carbon sinks (Kennedy *et al*., 2010). Shallower meadows are more depleted in ^{13}C than deep meadows (Fig. 2.d) except for the Solenzara mouth transect (Appendix S3). This increasing trend in isotopic signature with depth gradient (from -18.10 ± 0.02 ‰ to -12.53 ± 0.13 ‰), suggests that greater amounts of allochthonous C_{org} (non-seagrass-derived C_{org}) are buried in the shallow seagrass sediments. Shallow seagrass meadows exhibit higher productivity and canopy complexity than deep meadows (Serrano *et al.*, 2014, 2016b; Pergent-Martini *et al.*, 2020) which likely resulted in enhanced epiphytic and algal assemblages contributing up to 50% of the aboveground biomass in seagrass meadows (Borowitzka *et al*., 2006) but equally in the trapping of a higher content of fine allochthonous sediment particles contributing both to C_{org} accumulation, as reported in recent studies (Samper-Villareal *et al*., 2016; Serrano *et al*., 2016b; Mazarrasa *et al*., 2018).

In parallel, in estuarine ecosystems, seagrass meadows are generally subject to higher deposition of fine sediment particles resulting from terrestrial freshwater inputs (*i.e.* runoff and river discharge) and accumulated up to four-fold higher amounts of fine grain-grained particles compared to coastal meadows (Kennedy *et al*., 2010; Serrano *et al*., 2016c). The deposition of allochthonous fine sediment resulting from sestonic or freshwater terrestrial inputs led to a greater accumulation of allochthonous C_{org} which is corroborated by depleted values of $\delta^{13}C$ in sediments (Kennedy *et al*., 2010; Serrano *et al*., 2016c; Ricart *et al*., 2020). Therefore, the ^{13}C-depleted estuarine seagrass sediments found in this study could be explained by the significantly higher mud content (personal observation) probably resulting from the Golo and Tavignano rivers discharges. Moreover, meadows growing on sandy substrate generally located in sheltered areas (*i.e*. lower exposure to hydrodynamic energy) are characterized by an enhanced sediment deposition and a higher content of fine sediment particles compared to rocky meadows located in more exposed areas (Fonseca and Bell, 1998; Samper-Villarreal *et al*., 2016). Due to the difference in hydrodynamic exposure and sediment deposition between sandy and rocky meadows, the isotopic signature of rocky seagrass sediments was expected to be ^{13}C-enriched related to the low sediment deposition compared to sandy meadows. Yet, no significant changes in sedimentary $\delta^{13}C$ values were observed associated with matrix composition, contrary to findings in Ricart *et al.* (2017).

4.3. Variability in C_{inorg} stocks

In coastal temperate areas, seagrass meadows have been recognized for their high trapping and retention capacity of sediment particles (Jeudy de Grissac and Boudouresque, 1985; Gacia and Duarte, 2001). Sediments accumulated in the *P. oceanica* meadows may also be composed of a high percentage of biogenic carbonate particles resulting from calcifying biota associated with seagrass meadows (Boudouresque and Jeudy de Grissac, 1983; De Falco *et al*., 2000; Serrano *et al*., 2012). Through their high calcium carbonate ($CaCO_3$) production, *P. oceanica* meadows have been considered as one of the main 'carbonate factories' of the Mediterranean coastal areas (Canals and Ballesteros, 1997; De Falco *et al*., 2008; Mateu-Vicens *et al*., 2012). $CaCO_3$ production in *P. oceanica* meadows, estimated at between 68 to 1147 g $CaCO_3$ m^{-2} yr^{-1} (Canals and Ballesteros, 1997; Barrón *et al*., 2006; De Falco *et al*., 2008; Serrano *et al*., 2012), was in the range of other ecosystems such as algal communities (148.2-289.4 g $CaCO_3$ m^{-2} yr^{-1}), coralligenous habitats (169.6-464.6 g $CaCO_3$ m^{-2} yr^{-1}) and maërl beds (210.0 g $CaCO_3$ m^{-2} yr^{-1}; Canals and Ballesteros, 1997).

In this study, the $CaCO_3$ and C_{inorg} stocks significantly exhibited a high variability. With increasing water depth, seagrass sediments showed a significant increase in C_{inorg} stock (Fig. 4.b; Fig. 4.d). Seagrass habitats sheltered a rich community of organisms contributing to the production of biogenic $CaCO_3$ sediments (Jeudy de Grissac and Boudouresque, 1985; Fornos and Ahr, 1997; De Falco *et al*., 2008; Monnier et al., 2021a) but also imported significant amounts of $CaCO_3$ from adjacent sources such as coral reefs or terrestrial lithogenic areas (Saderne *et al*., 2019). In this study, the approximately two-fold higher C_{inorg} stock found in deep meadows (30-40 m depth; 41.73 ± 3.72 kg C_{inorg} m^{-2} in the top meter of matte) compared to shallow meadows (10-20 m depth; 18.60 ± 4.41 kg C_{inorg} m^{-2}) is likely related to the significant and dominant contribution of C_{inorg} allochthonous inputs in *P. oceanica* meadows. On the eastern coast of Corsica Island, the lower limit of *P. oceanica* meadows is characterized by the occurrence and the wide distribution of both biocenosis of coastal detritic bottoms and rhodolith beds (Bonacorsi, 2012; Valette-Sansevin *et al.*, 2019). Through their high $CaCO_3$ content (~90-95%; Fornos and Ahr, 1997; Lecca *et al.*, 2005; Brandano and Civitelli, 2007; Bonacorsi *et al.*, 2014) and their high production (210 g $CaCO_3$ m^{-2} yr^{-1}; Canals and Ballesteros, 1997), these calcareous habitats probably contribute to the C_{inorg} accumulation in seagrass sediments. Even though the distribution of biogenic carbonate production areas has been well identified in circalittoral zone along the Corsican coastline, some difficulties remain to clarify the fate and the contribution of this production to the seagrass carbon sink. However, the high proportion of free-living calcareous red algae (*e.g. Lithothamnion corallioides, Phymatolithon calcareum* and *Spongites fruticulosa*) found in *P. oceanica* matte at the lower limit explained these high C_{inorg} stocks. Sedimentary analysis performed at the lower limit of *P. oceanica* meadows located at Cap Corse (Corsica, France) showed that biogenic sand matrix constituted by high $CaCO_3$ content (~60%) was also characterized by the presence of free-living calcareous organisms due to the interactions of rhodolith beds with seagrass meadows (Bonacorsi, 2012). The concurrent export of $CaCO_3$ production from circalittoral coastal detritic bottoms and rhodolith beds toward the coastline due to marine currents and the trapping of fine to coarse carbonate fragments and particles by the *P. oceanica* meadows likely explains the higher C_{inorg} stock found at the lower limit of seagrass meadows and confirms the role of seagrass meadows as major allochthonous C_{inorg} burial sites (Saderne *et al.*, 2019). Furthermore, the high C_{inorg} stock reported in deep waters may be also related to the accumulation of C_{inorg} production resulting from the *P.*

oceanica meadows which colonized a lower bathymetric range before the sea level rise during the Pleistocene and Holocene periods (De Falco *et al*., 2011).

Seagrass meadows growing on sandy substrate exhibited a continuous increase in C_{inorg} stocks with level in the soil compared to rocky areas. These results are consistent with a previous work highlighting a negative correlation between $CaCO_3$ stock in *P. oceanica* sediments and the presence of a rocky matrix (Mateu-Vicens *et al*., 2012). Because photophilic algal communities exhibited one of the highest carbonate production rates among Mediterranean benthic ecosystems (34.73 g C_{inorg} m^{-2} yr^{-1}; Canals and Ballesteros, 1997), C_{inorg} deposition may be favored in seagrass sediments but only at short-term scale. The high erosion and low deposition of fine particles in areas exposed to hydrodynamic energy seems to be responsible for lower preservation of the C_{inorg} over time (Perry and Beavington-Penney, 2005). In addition, the $CaCO_3$ production in the *P. oceanica* meadows is mainly due to heterotrophic (*i.e.* light-independent) organisms, well suited to this ecosystem (*e.g.* Foraminifera, Bryozoa, Mollusca, Annelida, Arthropoda) but also to autotrophic and mixotrophic (*i.e.* light-dependent) organisms such as Rhodophyta (*e.g. Pneophyllum* sp., *Hydrolithon* sp., *Titanoderma* sp.; Canals and Ballesteros, 1997; Mateu-Vicens *et al*., 2012). Yet, though photo-independent calcareous organisms are quantitatively more important, light remains a major factor controlling the $CaCO_3$ production of these organisms within seagrass meadows. Heterotrophic organisms are significantly related to the presence of *P. oceanica* due to the formation of shelters and supports for many producers, as well as a higher pH (Mateu-Vicens *et al*., 2012; Hendriks *et al*., 2014). Consequently, lower shoot density and canopy complexity observed with decreasing light availability in estuarine environments (higher turbidity gradient) may explain the lower C_{inorg} stocks.

4.4. Implications for climate change mitigation

The C_{org} and C_{inorg} stocks combined with the morpho-bathymetric DTM of sea bottoms contributed to estimation of the amount of carbon stored within the sedimentary pool beneath *P. oceanica* meadows (Monnier *et al*., 2020a, 2020b). Over the entire area, the amounts of CO_{2e} stored have been estimated at 24.0 and 51.5 million t CO_{2e} for the top 100 cm and 250 cm of matte deposits, respectively, which is equivalent to 13.6 and 29.2 years of CO_2 emissions by the entire Corsican population. At regional scale, the C_{org} stock beneath *P. oceanica* meadows have been estimated at 63.2 ± 0.4 million t CO_{2e} (100 cm) and 135.5 ± 0.2 million t CO_{2e} (250 cm), that is to say the equivalent to 35.8 ± 0.2 and 76.8 ± 0.1 years of CO_2 emissions by the entire Corsican population (Appendix S7), constituting one of the most significant estimates of C_{org} stocks associated with *P. oceanica* meadows in the Mediterranean basin. Here, given the amount and the high variability of C_{inorg} stocks found in the seagrass sediments which may counterbalance the carbon sink role associated with this ecosystem (Howard *et al*., 2014b; Mazarrasa *et al*., 2015), additional estimates have been produced in this study to better appreciate its contribution to climate change mitigation. The capacity of seagrass meadows as long-term CO_2 sinks should be considered in relation to C_{inorg} production and storage to assess the net exchange of CO_2 (Howard *et al*., 2014b). At regional scale or worldwide, several studies have emphasized the necessity to include $CaCO_3$ production to determine the role of seagrass as carbon sink or source (Pergent *et al*., 2012; Howard *et al*., 2014b; Macreadie *et al*., 2017; Gullström *et al*., 2018). In spite of this recommendation, only one estimation has considered the role of the calcification process occurring in *P. oceanica* meadows to determine the carbon sink-source balance of this ecosystem. By associating the C_{org}-C_{inorg} stocks, this study exhibited that *P. oceanica* ecosystem could also represent a significant net CO_2 source (-27.2 to +14.3 Tg CO_2 yr^{-1}; Mateo and Serrano, 2012).

In this study, *P. oceanica* meadows have proved to be a net CO_{2e} sink except for the deeper bathymetric range (Figure 5). The overall amount of CO_{2e} stored was estimated at 11.1 million t CO_{2e} (100 cm) and 20.4 million t CO_{2e} (250 cm), corresponding to 6.3 and 11.6 years of CO_2 release by the Corsican population (Table 3). The overall net CO_{2e} stock found in the sedimentary deposits of *P. oceanica* meadows at regional scale have been estimated at 29.2 ± 0.2 million t CO_{2e} (top 100 cm) and 53.6 ± 0.2 million t CO_{2e} (top 250 cm) which is equivalent to 16.5 ± 0.1 and 30.4 ± 0.1 years of CO_2 release from the entire population of Corsica Island (Table 3). While the contribution of these carbon sinks seems to be reduced by almost half by considering the C_{org} and C_{inorg} stocks, these estimates should be interpreted and used with caution due to the fact that many processes may influence the precipitation, the dissolution, and the sedimentation of $CaCO_3$ and *in fine* the accumulation in seagrass sediments (Mazarrasa *et al*., 2015; Saderne *et al*., 2019). Indeed, the allochthonous inputs resulting from the interactions with adjacent sources may favour C_{inorg} deposition and increase the difficulty of assessing the role of this ecosystem as carbon sink or source (Kennedy *et al*., 2010; Saderne *et al*., 2019). Though seagrass meadows and more specifically *P. oceanica* meadows showed a high contribution in the C_{inorg} stock found in coastal ecosystems along Mediterranean shorelines (Hemminga and Duarte, 2000; Boudouresque *et al*., 2012; Serrano *et al*., 2012; Mazarrasa *et al*., 2015; Saderne et al., 2019), many adjacent benthic habitats (*e.g.* photophilic algal communities, coralligenous biocenosis, coastal detritic bottoms and rhodolith beds, coral reefs; Canals and Ballesteros, 1997; Bonacorsi *et al*., 2014) may contribute to the deposition of C_{inorg} in seagrass ecosystems (Saderne *et al*., 2019). In addition, after the simultaneous measurement of both C_{org} and C_{inorg} metabolic pathways, the $CaCO_3$ precipitation in seagrass ecosystems has proved to be related to the organic metabolic rates (Barrón *et al*., 2006; Hendricks *et al*., 2014; Saderne *et al*., 2019). Here, although the standing C_{org} and C_{inorg} stocks have been compared to produce a large-scale estimate of areas acting as carbon sink or source, a further research effort considering the

CO_2 emissions from C_{inorg} deposition and CO_2 burial from C_{org} sequestration in sediments is needed to achieve a better understanding of the role played by *P. oceanica* meadows in climate change mitigation.

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Table 1. Pearson's correlation matrix between the environmental and the biogeosedimentological parameters analyzed in the *P. oceanica* matte cores. Level of significance: *P≤0.05, **P≤0.01, ***P≤0.001; NS, P≥0.05; Significant correlations in bold (r value).

	Depth	Level	Density	%TOM	$\%C_{org}$	$\delta^{13}C$	$\%CaCO_3$	$\%C_{inorg}$
Depth		0.095	0.122	**-0.358**	-0.156	**0.660**	**0.745**	**0.745**
Level	NS		**0.575**	**-0.418**	**-0.364**	**0.285**	0.017	0.017
Density	NS	***		**-0.541**	**-0.498**	**0.241**	-0.061	-0.061
%TOM	***	***	***		**0.913**	**-0.397**	**-0.169**	**-0.169**
$\%C_{org}$	NS	***	***	***		**-0.157**	0.007	0.007
$\delta^{13}C$	***	***	**	***	*		**0.666**	**0.666**

%$CaCO_3$	***	NS	NS	*	NS	***		**1.000**
%C_{inorg}	***	NS	NS	*	NS	***	***	

Table 2. Estimates of net C_{org} and net CO_2 stock in the first 100 cm and 250 cm of *P. oceanica* sediments based on the balance between the C_{org} stock (CO_2 sink) and the C_{inorg} stock (CO_2 source). [(1)] Calculated by multiplying the C_{inorg} stock by 0.6 to meet the assumption that 0.6 moles of CO_2 are released per mole of $CaCO_3$ precipitated, then deducting this adjusted C_{inorg} value from the C_{org} stock to get the net CO_2 stock (in bold: net CO_2 source). [(2)] Calculated by multiplying the net C_{org} stock by 3.67.

100 cm		**C_{org} stock (kg C_{org} m^{-2})**	**C_{inorg} stock (kg C_{inorg} m^{-2})**	**net C_{org} stock [(1)] (kg C_{org} m^{-2})**	**net CO_{2e} stock [(2)] (kg CO_{2e} m^{-2})**
	n	**Mean ± S.E.**	**Mean ± S.E.**	**Mean ± S.E.**	**Mean ± S.E.**
Depth					
10 m	7	33.7 ± 3.9	10.3 ± 2.7	27.5 ± 4.6	100.9 ± 16.8
15 m	1	37.9 ± 0.0	18.5 ± 0.0	26.8 ± 0.0	98.4 ± 0.0
20 m	6	33.2 ± 2.3	27.7 ± 6.1	16.6 ± 2.8	61.0 ± 10.2
30 m	3	25.8 ± 5.7	46.8 ± 1[illegible].8	**-2.3 ± 6.7**	**-8.3 ± 24.6**
40 m	2	25.0 ± 7.0	41.0 ± 13.[illegible]	0.4 ± 15.3	1.4 ± 56.3
Substrate					
Sandy	5	38.8 ± 2.5	9.[illegible] ± [illegible].1	33.0 ± 2.8	121.0 ± 10.4
Rocky	2	20.8 ± 5.3	11.6 ± 7.6	13.8 ± 9.8	50.8 ± 36.1
Depositional environment					
Coastal	15	30.6 ± 2.3	27.6 ± 4.9	14.1 ± 4.1	51.8 ± 15.1
Estuary	4	35.4 ± 4.3	12.9 ± 6.2	27.7 ± 4.7	101.6 ± 17.1
Mean	**19**	**31.6 ± [illegible].0**	**24.5 ± 4.3**	**17.0 ± 3.6**	**62.3 ± 13.2**

250 cm		**C_{org} stock (kg C_{org} m^{-2})**	**C_{inorg} stock (kg C_{inorg} m^{-2})**	**net C_{org} stock [(1)] (kg C_{org} m^{-2})**	**net CO_{2e} stock [(2)] (kg CO_{2e} m^{-2})**
	n	**Mean ± S.E.**	**Mean ± S.E.**	**Mean ± S.E.**	**Mean ± S.E.**
Depth					
10 m	7	82.4 ± 9.6	29.8 ± 7.7	64.5 ± 8.3	236.8 ± 30.4
15 m	1	96.0 ± 0.0	42.8 ± 0.0	70.3 ± 0.0	258.2 ± 0.0
20 m	6	76.9 ± 8.3	71.8 ± 17.5	33.9 ± 13.1	124.3 ± 47.9
30 m	3	40.1 ± 10.7	101.2 ± 30.9	**-20.7 ± 16.4**	**-75.9 ± 60.4**
40 m	2	36.3 ± 12.4	102.4 ± 35.4	**-25.2 ± 33.7**	**-92.3 ± 123.7**
Substrate					
Sandy bottom	5	94.2 ± 7.3	35.7 ± 9.2	72.8 ± 6.8	267.2 ± 25.1
Rocky bottom	2	53.0 ± 13.4	15.2 ± 9.9	43.8 ± 19.3	160.8 ± 70.8
Depositional environment					
Coastal	15	65.9 ± 7.1	68.7 ± 11.9	24.7 ± 11.6	90.7 ± 42.7
Estuary	4	87.3 ± 12.8	30.0 ± 8.1	69.3 ± 9.9	254.3 ± 36.2
Mean	**19**	**70.4 ± 6.4**	**60.5 ± 10.2**	**34.1 ± 10.2**	**125.1 ± 37.4**

Table 3. Estimates of global C_{org} and CO_{2e} stocks in the first 100 cm and 250 cm of *P. oceanica* matte at site and regional scales by applying 'the rule of the 0.6' (Ware *et al*., 1992). (1) Estimates performed within the site (Fig. 5.a; Fig. 5.b). (2) Calculated by multiplying the annual CO_2 release per capita in France in 2018 (5.2 t CO_2 yr^{-1} $capita^{-1}$) by the total population of Corsica. (3) Estimates performed within the site (see Fig. 5.a and Fig. 5.b).

Study site				
Matte thickness	**Total C_{org} stock ($\times10^6$ t C_{org})**	**Total CO_{2e} stock ($\times10^6$ t CO_2)**	**Total CO_2 release per year in Corsica (2) ($\times10^6$ t CO_2 yr^{-1})**	**Equivalent in years of CO_2 emissions**
100 cm	3.0 (1)	11.1	1.8	6.3
250 cm	5.6 (1)	20.4		11.6

Corsica					
Matte thickness	**Mean ± S.E. C_{org} stock (kg C_{org} m^{-2})**	**Total C_{org} stock ($\times10^6$ t C_{org})**	**Total CO_{2e} stock ($\times10^6$ t CO_2)**	**Total CO_2 release per year in Corsica (2) ($\times10^6$ t CO_2 yr^{-1})**	**Equivalent in years of CO_2 emissions**
100 cm	14.8 ± 0.1 (3)	7.9 ± 0.1	29.2 ± 0.2	1.8	16.5 ± 0.1
250 cm	27.2 ± 0.1 (3)	14.6 ± 0.1	53.6 ± 0.2		30.4 ± 0.1

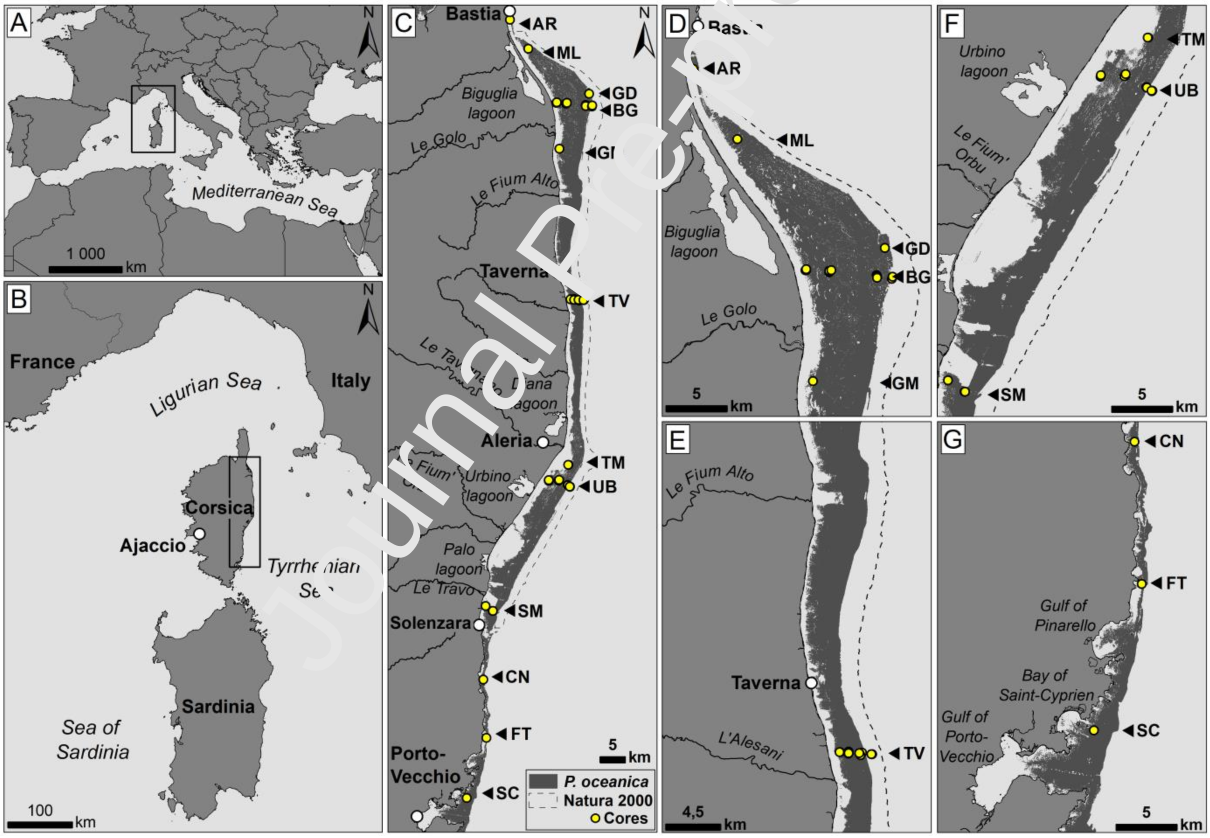


Figure 1. Location of the area of study on the eastern continental shelf of Corsica Island (a, b), distribution of the biocenosis of the *Posidonia oceanica* meadow and location of the sampling stations (c, d, e, f, g). AR: Arinella; ML: Marana lido; GD: Golo river delta; BG: Biguglia; GM: Golo river mouth; TV: Taverna; TM: Tavignano river mouth; UB: Urbino; SM: Solenzara river mouth; CN: Canella; FT: Fautea; SC: Saint-Cyprien.

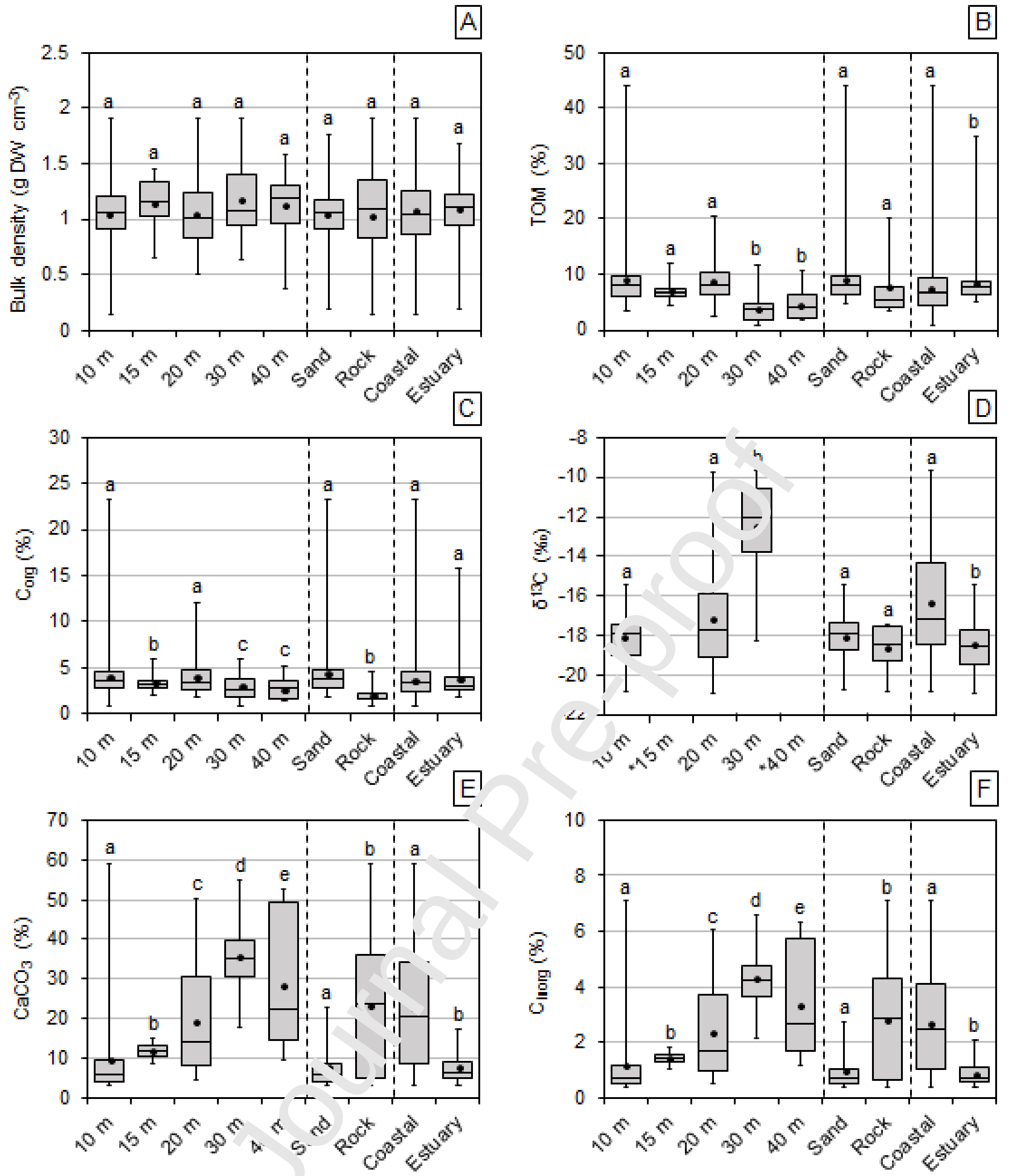


Figure 2. Box plots of (a) bulk density, (b) %TOM, (c) $\%C_{org}$, (d) $\delta^{13}C$ isotopic signatures of the sedimentary organic carbon (e) $\%CaCO_3$, and (f) $\%C_{inorg}$ at different depths, sediment matrix and depositional environment from *P. oceanica* meadow of east coast of Corsica (normalized for a top 100 cm thickness of matte). Black circles represent the mean value. Dissimilar letters denote significant differences between groups (ANOVA, p-value<0.05). *No data available.

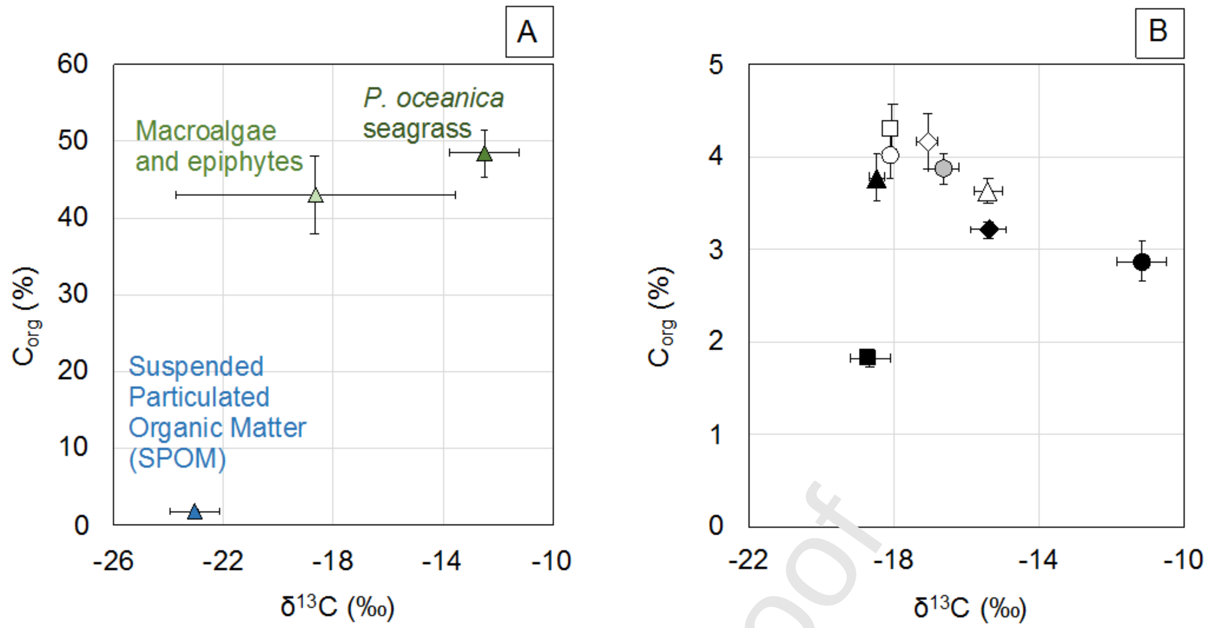


Figure 3. Mean (± S.E.) %C_{org} and $\delta^{13}C$ isotopic signature (‰) of potential organic sources (a) and in *P. oceanica* matte sampled at the study site (b) according to different environmental parameters such as depth (10 m: white circle; 20 m: grey circle; 30 m: black circle), sediment matrix (sand: white square; rock: black square), depositional environment (coastal: white triangle; estuary: black triangle) and soil depth considered (0-30 cm; white diamond; 30-100 cm: black diamond).

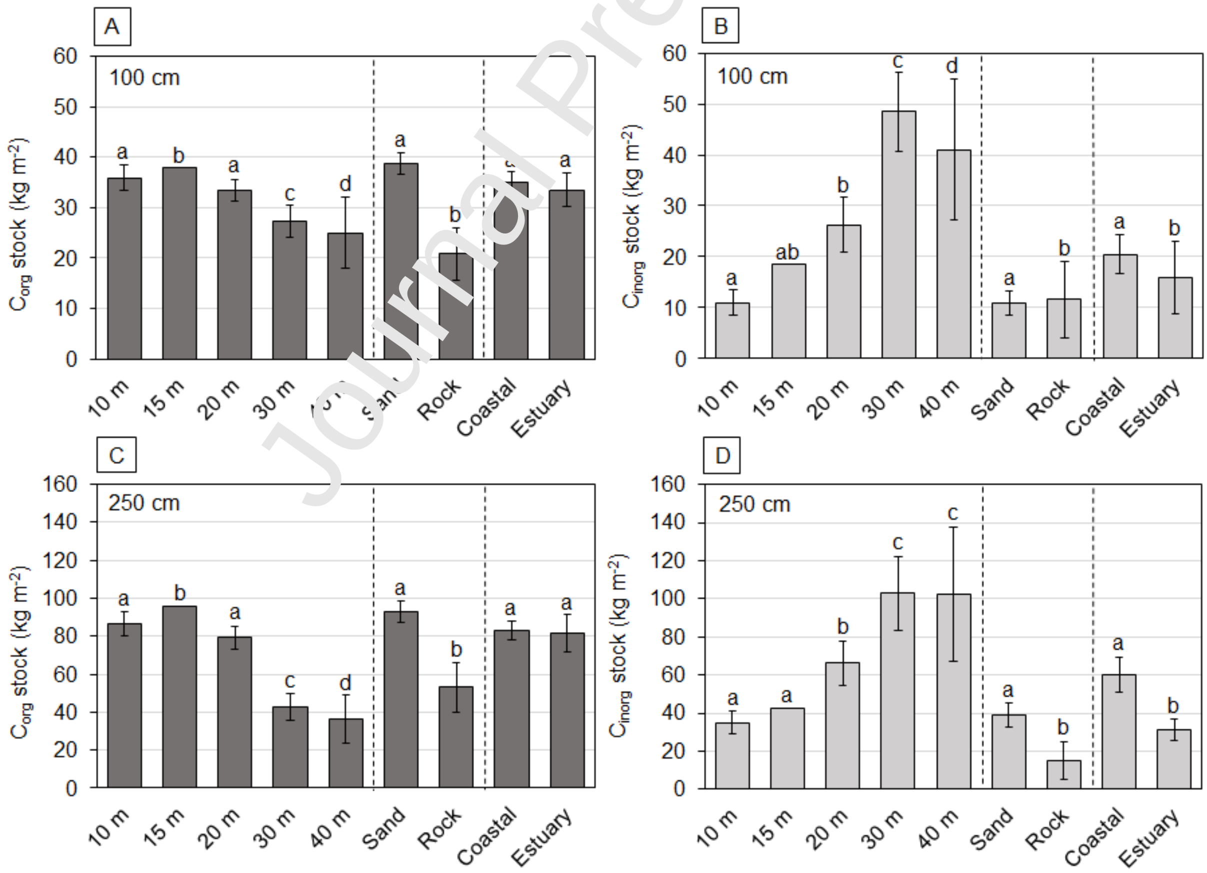


Figure 4. Mean (± S.E.) C_{org} and C_{inorg} stocks in the top 100 cm (a, b) and 250 cm (c, d) of *P. oceanica* matte determined at different depths, sediment matrix (sandy or rocky) and environmental influence (coastal or estuary).

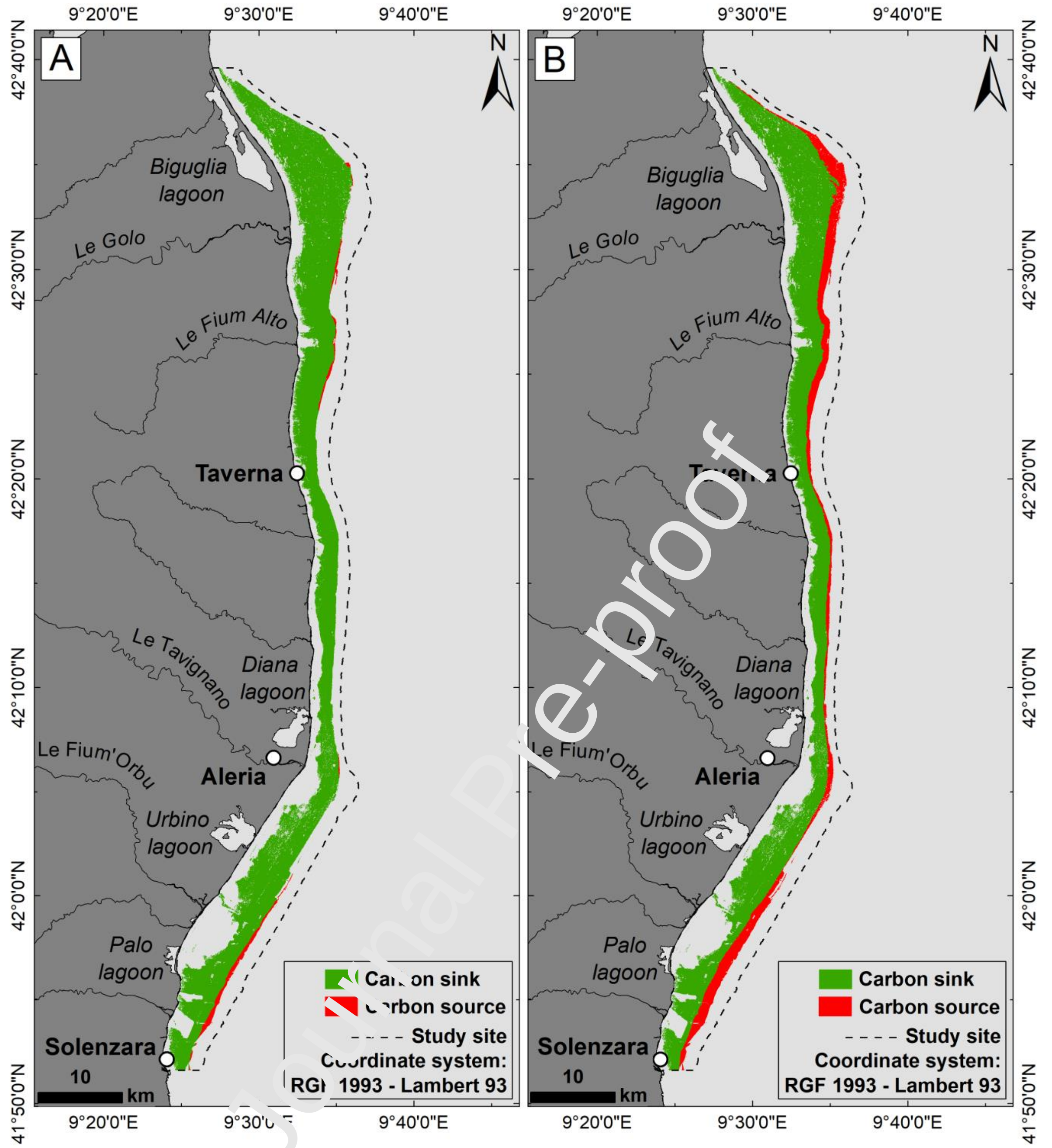


Figure 5. Contribution of the top 100 cm (a) and 250 cm (b) of *P. oceanica* matte as CO_2 sink (in green) or CO_2 source (in red) based on the balance between C_{org} stock and C_{inorg} stock. Calculated by multiplying the C_{inorg} stock value in each DTM raster cell (Appendix S6) by 0.6 to meet the assumption that 0.6 moles of CO_2 is released per mole of $CaCO_3$ precipitated, then deducting this adjusted C_{inorg} value from the C_{org} stock (Appendix S6) to get the net CO_2 stock.

CRediT author statement

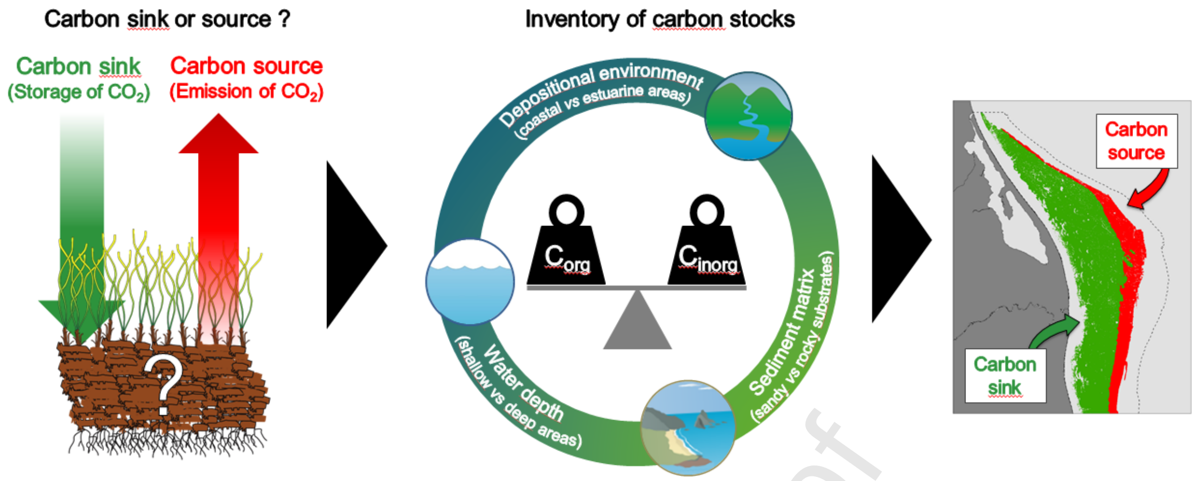
Briac Monnier: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - Review & Editing. **Gérard Pergent**: Validation, Investigation, Resources, Supervision, Resources, Writing - Review & Editing, Project administration, Funding acquisition. **Miguel Ángel Mateo**: Validation, Investigation, Supervision, Writing - Review & Editing. **Philippe Clabaut:** Investigation. **Christine Pergent-Martini**: Resources, Project administration, Funding acquisition.

Declaration of interests

☒ 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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Graphical abstract



Highlights

- Quantification of organic (C_{org}) and inorganic carbon (C_{inorg}) stocks is performed.
- Use of seafloor DEM provide reliable information to estimate the global stock.
- C_{org} and C_{inorg} stocks are crucial to assess the seagrass contribution as sink-source.
- For the first time, the carbon sink-source role of seagrass is modeled over 20 000 ha.