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A multi-approach inventory of the blue carbon stocks of *Posidonia oceanica* seagrass meadows: Large scale application in Calvi Bay (Corsica, NW Mediterranean)

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ABSTRACT

In Mediterranean, *Posidonia oceanica* develops a belowground complex structure ('matte') able to store large amounts of carbon over thousands of years. The inventory of blue carbon stocks requires the coupling of mapping techniques and *in situ* sediment sampling to assess the size and the variability of these stocks. This study aims to quantify the organic (C_{org}) and inorganic (C_{inorg}) carbon stocks in the *P. oceanica* matte of the Calvi Bay (Corsica) using sub-bottom profiler imagery and biogeochemical analysis of sediment cores. The matte thicknesses map (average ± SD: 2.2 m ± 0.4 m) coupled with marine benthic habitat cartography allows to estimate matte volume at 12 473 352 m^3. The cumulative stocks were assessed at 20.2–50.3 kg C_{org} m^{-2} and 26.6–58.7 kg C_{inorg} m^{-2} within the first meter of depth on matte (3632 ± 486 cal yr BP). The data contributed to estimate the overall carbon stocks at 389 994 t C_{org} and 615 558 t C_{inorg}, offering a new insight of the heterogeneity of blue carbon stocks in seagrass meadows. Variability of carbon storage capacity of matte influenced by substrate is discussed.

1. Introduction

Blue carbon was defined as the carbon fixed, sequestrated, stored or released from coastal and marine ecosystems such as tidal salt marshes, mangroves, coral reefs and seagrass meadows (Herr et al., 2012). Although these coastal habitats cover less than 2% of the ocean floor, their storage capacity represents about 50% of the carbon stored in ocean sediments (Nellemann et al., 2010). In opposition to forests, most of the organic carbon (C_{org}) sequestrated in coastal habitats is located within the soil and not in the living biomass (Murray et al., 2011). Indeed, the carbon burial rate is roughly fifty times higher in salt marshes, mangroves and seagrass meadows than in tropical, temperate or boreal forests (Mcleod et al., 2011). The high primary productivity of these ecosystems associated with the permanent vertical growth related to sediment deposition, contribute to the formation of organic-rich belowground reservoir recognized as carbon sinks. Among these coastal habitats, seagrass meadows are the third most active carbon sink after salt marshes and mangroves with 138 g C m^{-2} yr^{-1}, while covering the greatest area, *i.e.,* between 177 000 km^2 and 600 000 km^2 (Mcleod et al., 2011).

In the Mediterranean, the endemic seagrass *Posidonia oceanica* (L.) Delile develops a thick belowground formation called 'matte'. This soil organic structure reaching several meters in height is mainly composed of living and dead rhizomes and roots, with the interstices filled with sediment (Boudouresque and Jeudy de Grissac, 1983). The carbon stocks can remain buried over millennia and have been valued between

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40 and 770 kg C_{org} m^{-2} (Serrano et al., 2012c; 2016; Monnier et al., 2021a, 2022). The area covered by *P. oceanica* in coastal areas is estimated between 22 000 and 23 000 km^2 (Pergent-Martini et al., 2020; Traganos et al., 2022), making it one of the most important carbon sinks of the Mediterranean Sea (Pergent et al., 2012). Despite providing crucial ecosystem services (Vassallo et al., 2013; Bryan et al., 2016; Rigo et al., 2021), there is no doubt that *P. oceanica* has strongly declined in Mediterranean notably near the most anthropized areas like major harbours (*e.g.*, Barcelona, Marseille, Genoa, Naples) (Boudouresque et al., 2021; Telesca et al., 2015). This global regression is mainly related to anthropogenic pressure (*e.g.* coastal urbanisation, water quality decline, dredging, trawling, anchoring) and consequences of climate change (*e.g.* sea level rise) (Abadie et al., 2015; Boudouresque et al., 2009; Holon et al., 2015; Pergent et al., 2015, 2019). These impacts are not only responsible of local severe regression of the *P. oceanica* meadows, but also affect their carbon sink capacity and, in some cases, lead to the release of the carbon sequestrated (Mazarrasa et al., 2017).

During the last decades, recognizing the role of this Mediterranean seagrass species in the climate change mitigation, an increase number of studies have been focused to estimate the matte thickness and the storage capacity of this carbon sink. The estimates of the *P. oceanica* matte thicknesses is most often based on the use of low frequency acoustic sounders (Lo Iacono et al., 2008; Tomasello et al., 2009; Monnier et al., 2020a, 2021b). In addition to acoustic soundings, matte cores are used as ground-truthing data and their analysis allow to quantify the C_{org} and C_{inorg} stocks bringing additional information (*e.g.* organic and inorganic materials contents, sediment grain size, age; Serrano et al., 2012c, 2016a). This combined approach has been scarcely employed on large areas to obtain an accurate evaluation of the carbon stored by *P. oceanica* meadows (Monnier et al., 2020b, 2022; Piñeiro-Juncal et al., 2021). Here, using acoustic and seismic techniques and *in situ* sediment sampling, we aimed to assess the overall carbon stock found in *P. oceanica* meadow soils in the Calvi Bay, questioning variability of carbon storage capacity of matte influenced by substrate. We hypothesize that the carbon storage will be higher for seagrass meadows settled on sandy substrate than those growing on a rocky matrix.

2. Material and methods

2.1. Study site

The study site is located in Calvi Bay, a characteristic area of the north-western coast of the Corsica Island (France) covering about 22 km^2. Calvi Bay is closed by the Revellata Point on the western part (42°35′02′′N, 8°43′36′′E) and Spanu Point (42°36′02′′N, 8°47′53′′E) on the eastern part. The surface area occupied by *P. oceanica* meadows cover about around 6.2 km^2 between 3 and 37 m depth (Viala et al., 2021). The seagrass meadows represent the largest marine benthic habitats in the bay after unvegetated soft sediments and develop matte bioconstruction mainly on sandy substrate (Bay, 1984; Velimirov et al., 2016). In most places of the study area, meadows are continuous but local erosion ('intermattes') occurs due to anchoring mechanical destructions (Abadie et al., 2015, 2016). The meadow is qualified as healthy (Gobert et al., 2009), not subject to major anthropogenic stressors (except global change). Three areas were delimited following the nature of shoreline substratum: Punta Revelleta - Calvi (rocky substrate), Calvi beach (sandy substrate), Punta Caldanu - Punta Spano (rocky substrate) (Fig. 1). These three areas are different by the thickness of matte associated with the *P. oceanica* meadow. The sediment cores in *P. oceanica* meadows were performed in Stareso, Alga and Calvi stations located at a water depth of 20 m (Fig. 1) recognized as (i) the mean depth of seagrass meadows in this sector of Corsica

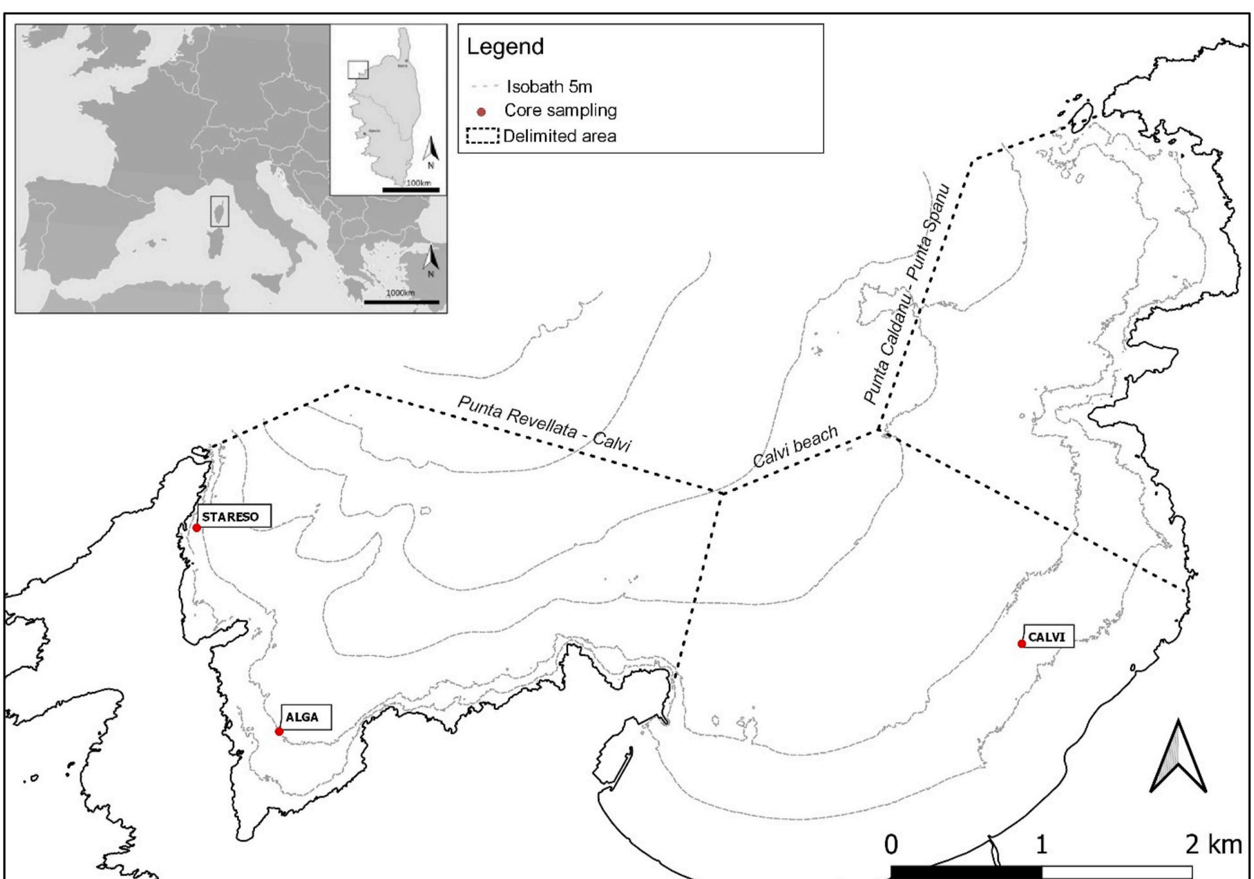

Fig. 1. Location of the study site, the delimited area and the sampling stations in Calvi Bay (red dots).

(Pergent-Martini et al., 2020) and (ii) the depth where the average carbon stocks have been recorded in *P. oceanica* meadows in Corsica (Monnier et al., 2022).

2.2. Seafloor classification

The cartography of marine benthic habitats was obtained using the seafloor classification technique developed by Viala et al. (2021). This method relies on the utilization of a multibeam echo sounder and specific bathymetric indices and classification algorithms to determine the seafloor nature (*i.e.,* seagrass, sediments, rocks). Acoustic data were acquired in July 2018 in Calvi Bay from 5 m to 120 m depth along more than 300 km measuring lines. The shallower part of the bay (<5 m depth) was manually classified using orthophotographs produced by the French Geographic National Institute in 2016.

2.3. Mapping of the matte thickness

Measurements of the matte thickness is derived from seismic reflection data obtained with the high-resolution sub-bottom profiler (SBP) Echoes 10 000 developed by iXblue. This SBP is a chirp system, ranging from 5 to 15 kHz, allowing 3D mapping of sediment architecture and geological features, by gathering 2D vertical profiles of the sediment layers below the seafloor. Depending on sediment types, penetration ranges from few meters in rough and compact sandy environments to several tens of metres below the sediments surface, and allows to detect the matte thickness on seismic profiles. The acoustic systems consisted in a transmit/receive array connected to a power amplifier unit and a laptop embarked on the *Seaviews One*, a 6 m-long vessel specially designed for hydrographic surveys. Data were acquired and recorded using Delph Seismic software developed by iXblue. Data positioning was operated by a Trimble BTX982 GNSS providing a centimetre positioning accuracy. Additionally, a GNSS North RTKITE was used in base mode and place at the Stareso research station during the whole acoustic acquisition to obtain a centimetre precision of the positioning of acoustic data.

Acquisition of seismic reflexion data was performed during three days in May 2019. A total of 52 transects were made to cover the whole surface of the *P. oceanica* meadows in the bay. The navigation was operated by a Raymarine ACU 200 autopilot synchronised with the RTK GNSS using ViewMap, a Geographic Information System (GIS) and navigation software developed by Seaviews which allows to trace and follow precise trajectories during acoustic data acquisition. The whole navigation system has an accuracy of 0.5 m to follow trajectories.

Matte thickness derivated from seismic reflexion data was processed in the ViewSingleBeam software developed by Seaviews. An integrative computation of the acoustic data is performed following four steps: (i) detection of the signal envelope to remove the modulations due to the frequency of the signal emitted; (ii) averaging signals; (iii) detection of the heights Ha and Hb corresponding to 50% and 40% of the maximum energy respectively (Fig. 2); (iv) calculation of the matte thickness. Finally, a digital elevation model (DEM) was obtained and exported to ViewMap software developed by Seaviews.

Matte volumes were calculated using ViewMap ('Volume calculator' tool). It was computed at first for the whole DEM and refined using the map of marine benthic habitats made in 2018 (Fig. 1). The global map was then divided in three areas corresponding to three representative meadows: Punta Revellata-Calvi, Calvi beach and Punta Caldanu-Punta Spanu.

2.4. Collection and subsampling of sediment cores

The sampling of sediment cores was performed between June and September 2019 in Stareso, Alga and Calvi stations (Fig. 1). For each station, one core was collected using 200 cm-long PVC tubes (internal diameter: 8 cm, wall thickness: 0.2 cm). Coring tubes were inserted manually into the seagrass sediment using a metal hammer (Fig. 3). Due to physical coring process, sediment compaction was estimated at 18 ± 3% (mean ± S.D.; Howard et al., 2014). This calculation is based on a simple compaction ratio using depth of the sediment inside and outside the core before extraction (Howard et al., 2014). The coring tubes were then vacuum sealed, extracted and stored vertically at −4 °C before analysis. In the laboratory, cores were opened by cutting the core tubes on either side throughout the length of the core with an electric saw. Each core was then subsampled in 1 cm-thick slices taken at 5 cm intervals throughout the core. Each sample was dried at 60 °C for 24–48 h

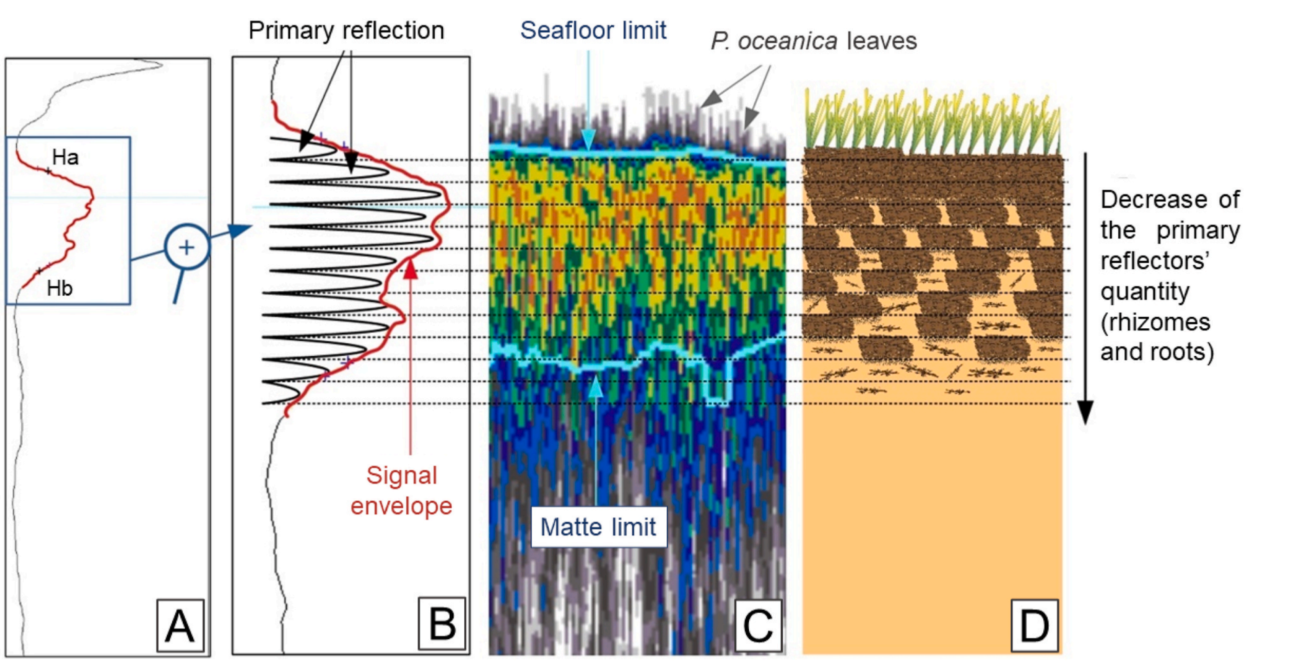

Fig. 2. Interpretation of the soil acoustic data according to the matte structure. Ha and Hb correspond to 50% and 40% of the maximum energy respectively. A) Vertical acoustic signal of a ping; B) zoom on the part of the signal corresponding to the matte; C) correspondence with the matte limit on the sonograms; D) schematic description of the soil linked with the sonogram.

Fig. 3. A) Vertical matte wall of a P. oceanica meadow resulting from its erosion by marine currents, B) core sampling in one of the station and, C) core processing in the laboratory.

to measure the dry weight and the sediment dry bulk density (ρ_b; g cm^{-3}) corresponding to dry weight of sediment per volume of each core sample.

2.5. Radiocarbon dating and sediment accretion rate

Radiocarbon dating (^{14}C) was used to estimate the matte age over the three stations. Radiocarbon measurements were achieved using the ARTEMIS Accelerator Mass Spectrometer of the *Centre de Datation par le RadioCarbone, UMR 5138 "Archéométrie et Archéologie"* (Lyon, France). The samples of *P. oceanica* tissues (fibres, living and dead rhizomes and roots) (~1 g) were selected at similar depths in the soil (*i.e.,* 40 cm, 80 cm and core bottom (ranging from 99 cm to 156 cm). Radiocarbon calibrated ages are presented as calibrated year before physics (cal. yr BP) with 0 cal yr BP being AD 1950. Conventional radiocarbon ages obtained were calibrated using the OxCal (4.3.2; Bronk Ramsey, 2017) using the Marine13 curve (marine reservoir correction (DR) of 400 years, Delta R = 0). Sediment accretion rate (SAR; mm yr^{-1}) between two particular depths at each location was calculated with the calibrated age by performing linear age-depth models with the clam.R package.

2.6. Biogeochemical analysis

Dry samples were separated into four different fractions by sieving (2 mm mesh): coarse organic fraction (COM, >2 mm, composed by *Posidonia* fibres), coarse mineral fraction (>2 mm, composed by gravel and coarse particles), coarse calcium carbonate fraction ($CaCO_3$ >2 mm, composed by shell debris) and fine fraction (<2 mm). Each fraction was respectively weighed, and isolated.

The organic and $CaCO_3$ contents were estimated through the loss on ignition (LOI) method (Heiri et al., 2001). Fine fraction (<2 mm) and COM (>2 mm) were homogenised and milled into a powder (Polymix grinder; 0.5 mm mesh; University of Corsica). Samples (3 g) were placed in crucibles, dried at 80 °C (12 h) and successively combusted at 550 °C (5 h) and 950 °C (2 h) in a muffle furnace. Between each combustion, the weight loss was measured to determine the total organic matter (%TOM) and the fine calcium carbonate (%$CaCO_3$ <2 mm) content (Heiri et al., 2001). The total $CaCO_3$ content corresponds to the fine $CaCO_3$ (<2 mm) and coarse $CaCO_3$ (>2 mm) contents.

The C_{org} contents and sources of organic matter were measured by performing elemental (%C_{org}) and isotopic analysis ($\delta^{13}C$) every 10 cm intervals (Table S1) using the similar homogenised and grinded samples (see above). After $CaCO_3$ removal by sediment acidification (HCl 1N), analyses were performed using a vario Microcube Elemental Analyser (VarioMicro, Elementar, Germany) coupled with an IsoPrime Isotope Ratio Mass Spectrometer (Isoprime 100, Isoprime, UK) University of Liège. Substances of known composition (glycine) and of substances certified by the atomic energy agency (IAEA) were used as standard. Elemental data were expressed as a percentage of dry mass (%C_{org}). 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 $^{13}C/^{12}C$).

2.7. Evaluation of total carbon stock

The sedimentary C_{org} and C_{inorg} stocks in the first 100 cm of matte were estimated for each core. The amount of C_{org} and C_{inorg} in each core section of were estimated using the following equation (**Eq. (1)**; Howard et al., 2014; Jiang et al., 2019):

$$\text{Carbon stock in core section (g cm}^{-2}) = \rho_b * (\%C/100) * S_T \quad \textbf{Eq.} \quad 1$$

with ρ_b, the sediment dry bulk density (g cm^{-3}), %C, the percentage of C_{org} or C_{inorg} measured in the section and S_T, the thickness of the section (cm). In this study, each 1 cm-thick subsample collected every 5 cm along the core was extrapolated to obtain similar section thickness (*i. e.,* 5 cm). The cumulative C_{org} and C_{inorg} stock per core was computed by adding the value of each section and normalized to stratigraphic depths of 100 cm to allow comparisons with other studies and to the mean thickness of matte reported in the study site. The total carbon was converted into the units commonly used in carbon stock assessment and the average amount of carbon in a core were estimated.

The estimates of C_{org} and C_{inorg} stored in the matte of *P. oceanica* meadows were performed by using (i) the DEM of matte thickness (see above) and (ii) the mean linear regression equations of cumulative C_{org} (**Eq. (2)**) and C_{inorg} stocks (**Eq. (3)**) considering the three cores.

$$C_{org} \text{ stock} = 0.3129 \times \text{Matte thickness} + 0.1727 \quad \textbf{Eq. } 2$$

$$C_{inorg} \text{ stock} = 0.5141 \times \text{Matte thickness} + 3.9441 \quad \textbf{Eq. } 3$$

The C_{org} and C_{inorg} stocks within the study site were produced by integrating the linear regression formulae in the DEM ('Raster Calculator' tool; ArcGIS® 10.0; ESRI, 2011) allowing to obtain a C_{org} and C_{inorg} stock value for each cell of the raster layer.

2.8. Statistics

Statistical analyses were performed using R version 3.5.3 (R Core Team, 2018). The normality of parameter values was tested using Shapiro-Wilk test. The relationships between the variables were analysed using Spearman correlation coefficient. The correlation coefficient was calculated together with p-values to determine the significance and strength of each relationship. Principal Component Analysis (PCA) was conducted to test the influence of sediment features (*i.e.,* density and depth in the soil), on sediment composition (%C_{org}, %C_{inorg}, %TOM, %$CaCO_3$, and isotopic signal ($\delta^{13}C$)).

3. Results

3.1. Benthic habitats

Among the variety of marine habitats maps, *P. oceanica* and *Cymodocea nodosa* seagrass meadows and dead matte cover an area of 7.3 km^2 in Calvi Bay (Fig. 4). *P. oceanica* meadows were found from 2 m to 40 m depth. They are settled on hard substrates in areas such as the surrounding of Punta Spanu and Punta Caldanu while the most extensive meadows were on soft substrates (Fig. 4). Living *P. oceanica* meadows have a surface of 6 km^2 while dead matte areas cover an area of 0.2 km^2.

3.2. Thickness and volume of *P. oceanica* matte

The average thickness of matte was assessed at 2.2 m ± 0.4 m and reach in maximum 5.0 m (Fig. 5). Highest thicknesses were observed at the deeper bathymetric range occupied of the *P. oceanica* meadow off Calvi beach. Globally, matte was thicker in the central and eastern part of the bay than in the western part (Table 1). The total matte volume calculated in Calvi Bay was 12 473 352 m^3. The highest volume of matte (6 585 112 m^3 and 52.8%) was observed in the area of Calvi beach. However, Punta Revellata-Calvi and Punta Caldanu-Punta Spanu meadows showed similar volume of matte (3 108 454 m^3 and 2 764 035 m^3, respectively; Fig. 5).

3.3. Radiocarbon dating and sediment accretion rate

The estimation of the matte age by ^{14}C dating was performed on three cores of a length ranging from 99 cm to 156 cm, taking into account the compaction correction factor. Samples were taken at three different depths in each core. The age of the deepest samples has been dated of 3781 ± 35 cal yr BP at 99 cm depth for Calvi station, 4193 ± 34 cal yr BP at 156 cm depth in Alga station and 4399 ± 32 cal yr BP at 142 cm depth in Stareso station (Fig. 6). The mean age at 1 m depth is estimated at 3632 ± 466 cal yr BP with a maximum age in Stareso station with a value of 4026 ± 32 cal yr BP. The age-depth models reveal a regular sediment accretion rate (SAR) in Alga and Calvi stations whereas the growth of the meadow in Stareso station appears to follow a

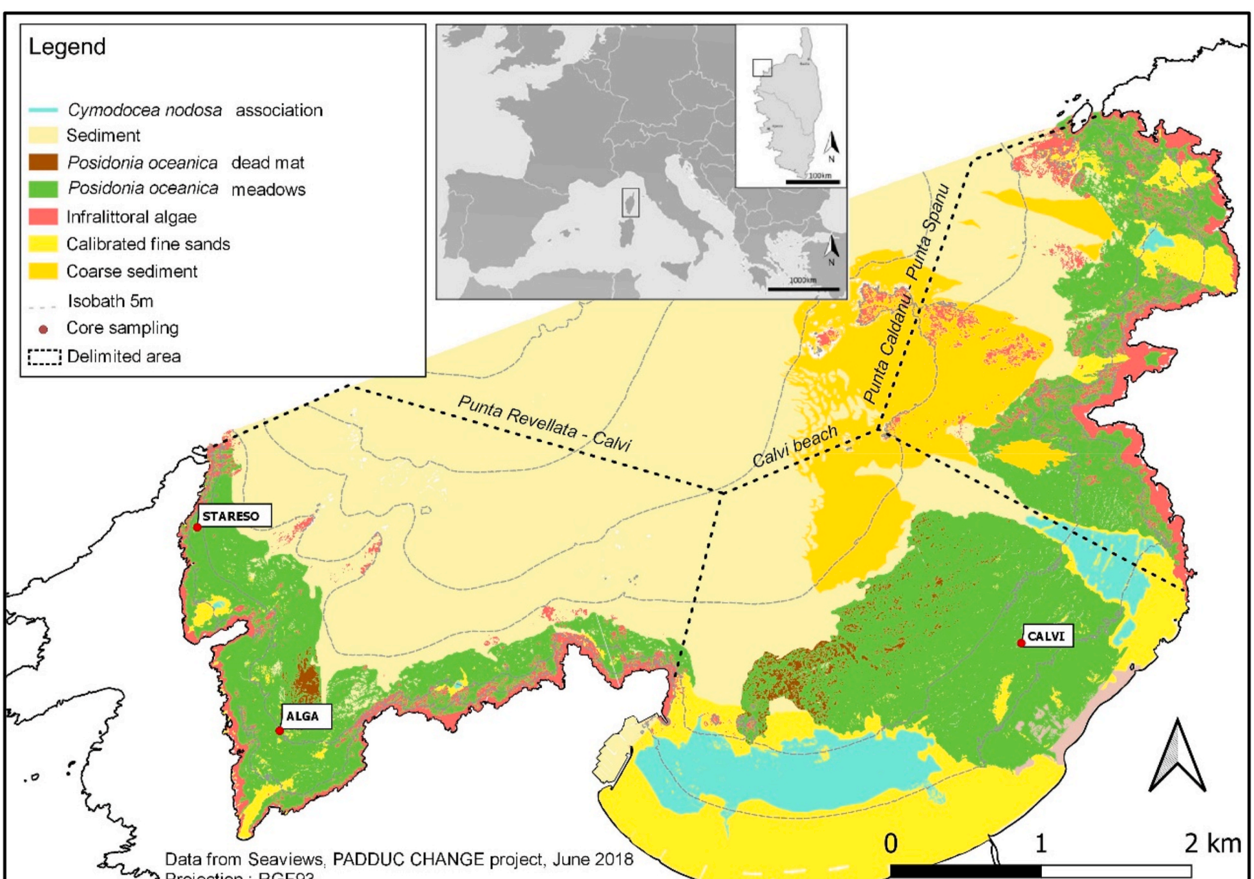

Fig. 4. Map of marine benthic habitats in Calvi Bay.

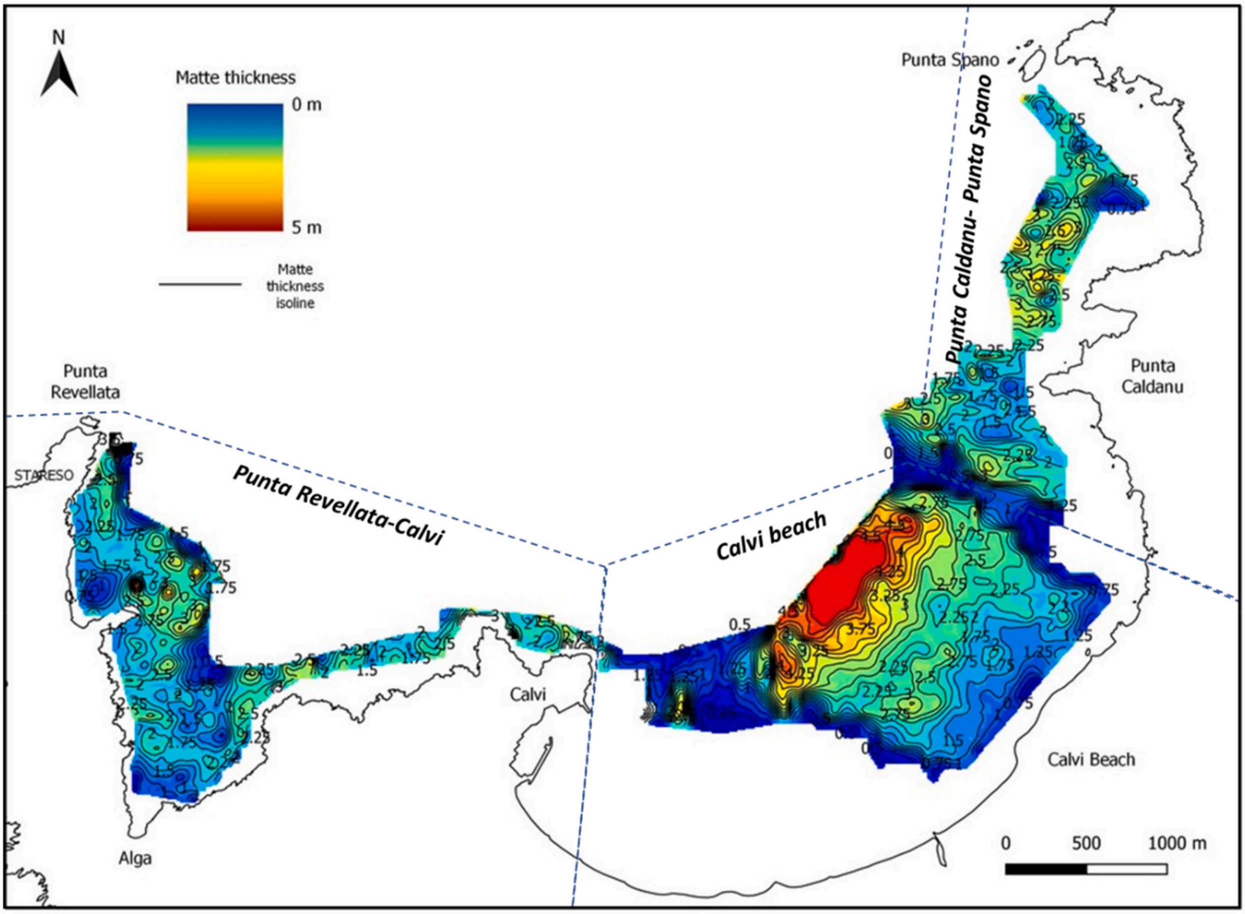

Fig. 5. Map of the matte thicknesses of P. oceanica meadows in Calvi Bay.

Table 1
Surface area occupied by P. oceanica meadows, volume of matte, mean thickness and density of matte in the Calvi Bay according to the three meadows of the area.

Area	Surface of *P. oceanica* meadows (m^2)	Matte volume (m^3)	Mean matte thickness (m)	Percentage of total volume (%)
Punta Revellata-Calvi	1 656 482	3108 454	1.9	24.9
Calvi beach	2 541 282	6585 112	2.6	52.8
Punta Caldanu-Punta Spanu	1 239 099	2779 786	2.2	22.3
Total	**5 436 863**	**12 473 352**	**2.2**	**100.0**

less linear pattern (Fig. 6; Table 2). In Calvi Bay, the mean SAR have been estimated at 0.3 ± 0.1 mm yr^{-1} (Table 2).

3.4. Biogeochemical features

The biogeochemical composition profiles of the *P. oceanica* matte varies significantly with depth in the soil and through the different stations (Fig. 7). The coarse mineral content is high on the 0–30 cm and 70–100 cm sections of matte in Stareso (10.1% and 6.4%, respectively) and on the deep sections of core sampled in Calvi station notably between 105 and 142 cm (between 2.1 and 8.3%). Alga station has a very low content in coarse mineral fraction along core (from 0.1 to 0.8%).

The coarse $CaCO_3$ fraction (>2 mm) occurred mainly in the deepest section of Stareso (41.4% at 138–151 cm depth) and Calvi stations (39.8% at 118–124 cm depth). The higher content in coarse organic fraction (%COM), composed by *P. oceanica* and macrophytes remains over 2 mm, is found mainly on the upper part of the core down to about 30 cm. In contrast, the fine fraction of the sediment, followed an opposite trend and is more widely represented over the entire length of the core for all sites.

In a PCA model, the Stareso and Alga stations were grouped separately from the Calvi site (Fig. 8a; Table 3). The PCA model explained a large part of the variation with eigenvalues of 0.46 for PC1 and 0.32 for PC2 (Fig. 8b). The sediment features such as dry-bulk density showed negative correlation with C_{org} and TOM content while the core level was more related to organic matter (%).

For comparison of different parameters, only the first meter of each core was considered. Considering all cores, the bulk density values ranged from 0.6 to 1.5 g cm^{-3} with an average value of 1.0 ± 0.2 g cm^{-3} (Fig. 9). The dry-bulk density increased significantly (p-value = 0.003) with depth in sediment, from 0.8 ± 0.2 to 1.1 ± 0.3 g cm^{-3} (Fig. 9). Vertical trends (surface to 100 cm depth in the core) showed that the % TOM decreased significantly (p-value = 0.007) with depth, from 8.5 ± 3.3% to 7.1 ± 2.0%. $CaCO_3$ contents values ranged from 39.6 ± 21.4% to 56.8 ± 22.4%. C_{inorg} content values ranged from 4.8 ± 2.7% to 6.4 ± 2.8%. C_{org} content values ranged from 5.9 ± 6.4% to 2.8 ± 1.3%. The $CaCO_3$, C_{inorg}, C_{org} contents in the matte follow any specific distribution pattern within soil depth except in Stareso where a strict increase of C_{inorg} content is observed at 140 cm depth that corresponds to a bioconstruction made up of *Corallinacea* sp.

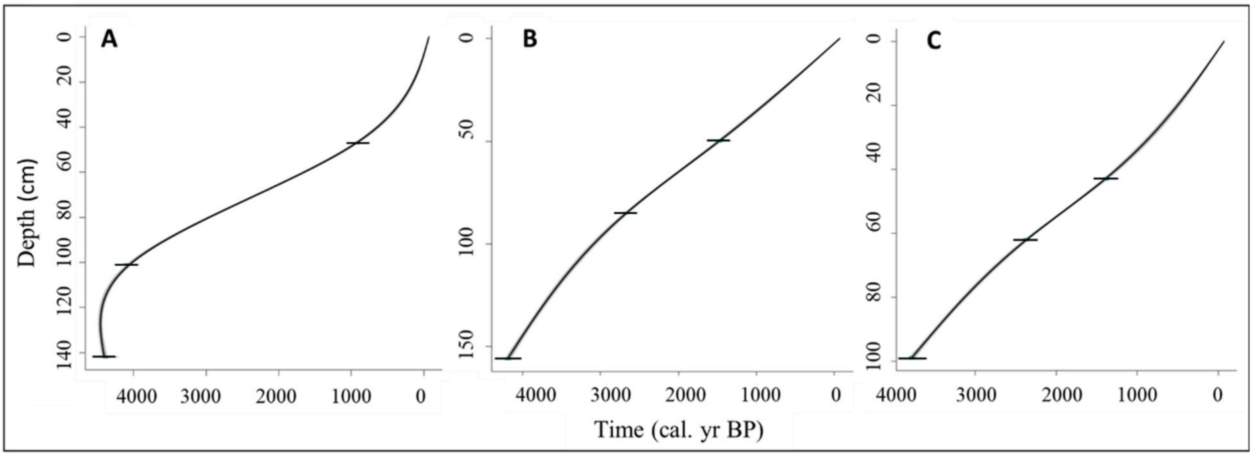

Fig. 6. Chronostratigraphic age-depth models of matte in Stareso (A), Alga (B) and Calvi (C) stations.

Table 2
Mean (±S.D.) sediment accretion rates (mm yr^{-1}) of the *P. oceanica* matte normalized over 30 cm, 50 cm and 100 cm thick deposits.

	30 cm	50 cm	100 cm
Stareso	0.80 ± 0.26	0.59 ± 0.33	0.39 ± 0.31
Alga	0.33 ± 0.01	0.32 ± 0.01	0.32 ± 0.03
Calvi	0.33 ± 0.03	0.29 ± 0.06	0.27 ± 0.05

3.5. *Organic and inorganic carbon stocks*

The C_{org} stocks on the first meter of the *P. oceanica* matte ranged from 20.2 kg m^{-2} (Stareso) to 50.3 kg C_{org} m^{-2} (Alga) with an average value estimated at 32.1 ± 9.2 kg m^{-2} (Fig. 10a). The C_{inorg} stocks on the first meter of the *P. oceanica* matte ranged from 26.6 kg m^{-2} (Calvi) to 58.7 kg m^{-2} (Stareso) and reached in mean 46.7 ± 10.1 kg m^{-2} (Fig. 10b). Considering the mean first 220 cm of matte (mean thickness observed in the Calvi Bay), the mean C_{org} and C_{inorg} stocks reach 60.1 ± 11.7 kg m^{-2} and 128.7 ± 27.5 kg m^{-2}, respectively. Upscaling of C_{org} and C_{inorg} stocks was undertaken after integrating the respective functions describing the cumulative C_{org} and C_{inorg} stocks into the DEM raster mosaic of matte thicknesses (Fig. 5). The total amount of C_{org} and C_{inorg} stored in *P. oceanica* matte have been estimated at 389 994 t and 615 558 t, respectively.

The isotopic composition of C_{org} found in the first 100 cm of matte ranged between −16.4 and −20.5‰ with an average value of −17.9 ± 1.0‰ (Fig. 11). The seagrass sediment of Stareso (−17.6 ± 1.1‰; p = 0.0025; Fig. 11a) and Alga stations (−17.3 ± 0.5‰; p = 0.0001; Fig. 11b) exhibit significantly higher $\delta^{13}C$ values compared to Calvi station (−18.8 ± 0.3‰; Fig. 11c). Over the first meter of sediment, $\delta^{13}C$ values decreased continuously from the upper (0–30 cm) to the lower section (70–100 cm) of the Alga and Calvi cores (−17.8 ± 0.9‰ to 18.4 ± 0.9‰), except for Stareso one where isotopic signature increases with soil depth.

4. Discussion

4.1. *Record of ecological succession in seagrass sediments*

Similarly, to other studies in the northwestern Mediterranean (Aloïsi et al., 1978; Boudouresque 1981; Serrano et al., 2012c; Monnier et al.,

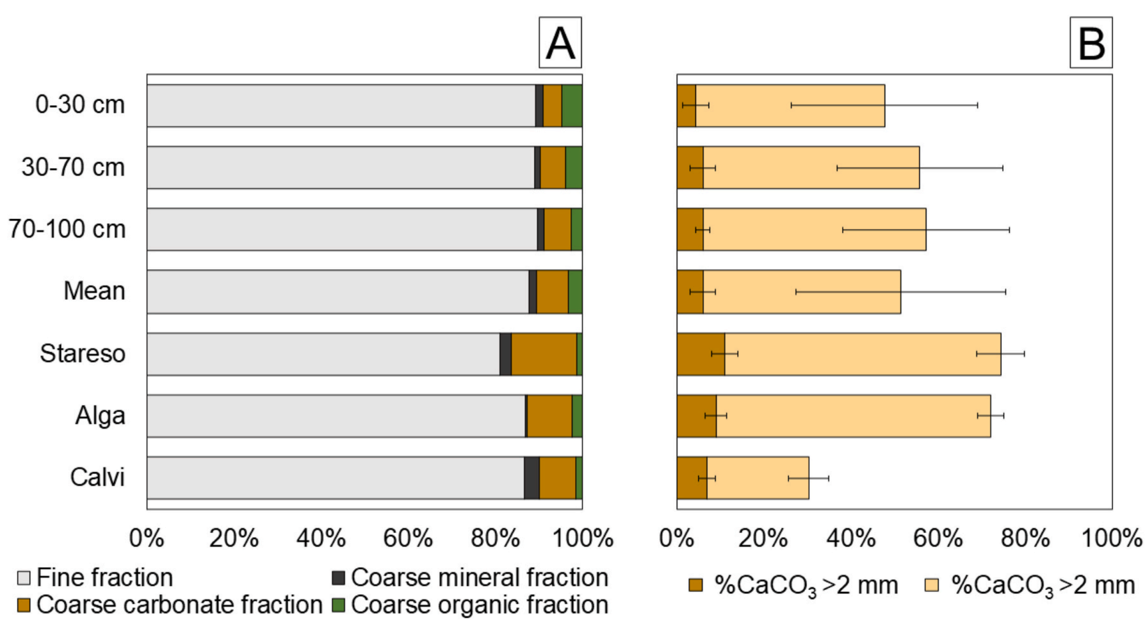

Fig. 7. Mean values for the different sedimentary fraction (left) and carbonate content (right) in the 0–30 cm, 30–70 cm and 70–100 cm fractions and in the different stations. Values are expressed as percentage of the total sample dry weight.

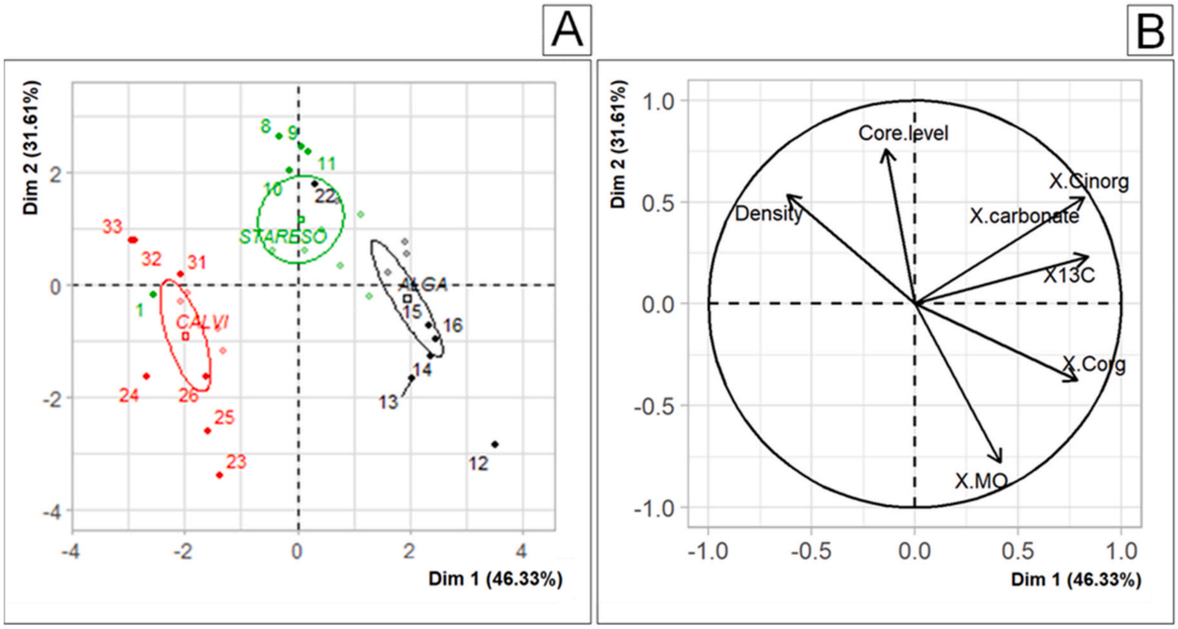

Fig. 8. Principal component analysis (PCA) showing the three stations (in green: Stareso, in black: Alga, in red: Calvi), the variables (Density = dry bulk density (ρ_b), Core level = level in the soil, XMO = %TOM, Xcarbonate = %$CaCO_3$, XC_{org} = %C_{org}, X C_{inorg} = %C_{inorg}, X13C = $\delta^{13}C$ isotopic signal). (A) Plot of individuals, and (B) plot of variables.

Table 3
Spearman correlation matrix between the environmental and the biogeosedimentological parameters analysed in the P. oceanica matte cores. Level of significance: *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001, NS P ≥ 0.05. In bold, significant Number corresponds to correlation coefficient.

	Level	Density	%TOM	%$CaCO_3$	%C_{inorg}	% C_{org}	$\delta^{13}C$
Level		**0.531**	**−0.474**	0.320	0.320	−0.214	−0.008
Density	**		**−0.575**	−0.249	−0.249	**−0.637**	**−0.356**
%TOM	**	***		−0.175	−0.175	**0.682**	0.201
% $CaCO_3$	NS	NS	NS		**1.000**	**0.410**	**0.167**
%C_{inorg}	NS	NS	NS	***		**0.410**	**0.637**
%C_{org}	NS	***	***	*	**		**0.580**
$\delta^{13}C$	NS	*	NS	***	***	***	

2021a, 2021b), the radiocarbon dating performed confirms the settlement of *P. oceanica* meadows in Calvi Bay during the Holocene period. The endemic seagrass is present all along the coast in the infralittoral area and is thus a witness of the matte formation. The core taken in Stareso station is characterized by the presence of a calcareous bioconcretion at 100 cm depth in the soil correspond at an age of 4026 ± 32 cal yr BP. On previous study, a similar bioconcretion made up of *Corallinacea* sp. dated of 3900 ± 100 cal yr BP has been revealed on the matte walls of intermattes at around 100 cm depth (Boudouresque 1981). This result shows that *P. oceanica* meadows settled in this part of the Calvi Bay have been replaced by another climax based on encrusting *Corallinacea* sp. and then recolonized. Several hypotheses likely linked to climate trends explain this succession. The occurrence of this calcareous formation coincides with the 4.2 kyr climatic event, corresponding to an important climatic aridification period. Thus, the ecological succession from *P. oceanica* meadows to the *Corallinacea* sp. formation may be explained by a decrease in seagrass meadows vitality associated with an increase in sea surface temperature. The decline of the *P. oceanica* meadows may resulted from an increase in water turbidity linked to a rejection of massive terrigenous elements originating from massive forest fires in Corsica during this climatic period. The lower values of ^{13}C observed on the Calvi station (allochthonous contributions) and the presence of small coal fragments at around 100 cm depth (*i.e.*, 4000 cal yr BP) on the Calvi station located near an estuary seems to confirm this hypothesis (Fig. 1).

4.2. *Variability in sediment accretion rate*

The mean matte thickness observed in this study showed a high variability between the three different sites. The highest value (6 m) on the site of Calvi beach can be explained by the movement of the deeper limit of the *P. oceanica* meadows over the last millennia following the sea level rising resulting in buried matte deeper than the current limits of the seagrass meadow. Another aspect could be the higher sedimentation rate due to the inputs of the two rivers flowing in this area, leading to a higher vertical growth rate of *P. oceanica*. The two other areas (Punta Revellata-Calvi and Punta Caldanu-Punta Spanu) had a lower mean matte thickness of 1.9 m and 2.2 m respectively that may reflect the presence of a rocky seabed beneath a shallow layer of sediments and matte.

The matte thicknesses estimated across Calvi Bay are consistent with regional values observed notably on the east coast of Corsica (2.52 m; Monnier et al., 2021b) and those recorded in Italy (1.6 m; Gulf of Palermo; Tomasello et al., 2009) and Spain (4.5 m; Port Lligat; Lo Iacono et al., 2008). The results obtained in this study confirm that seismic reflection method and the use of sub-bottom profilers are of particular interest to size the matte thickness of *P. oceanica* meadows.

The edification of *P. oceanica* matte is due to its vertical growth allowed by orthotropic rhizomes fighting against burial (Pergent et al., 1994) leading to the sequestration of high amounts of carbon. The accretion rate integrates the vertical growth rate as well as erosion and changes in growth. The accretion rate obtained in this study (between

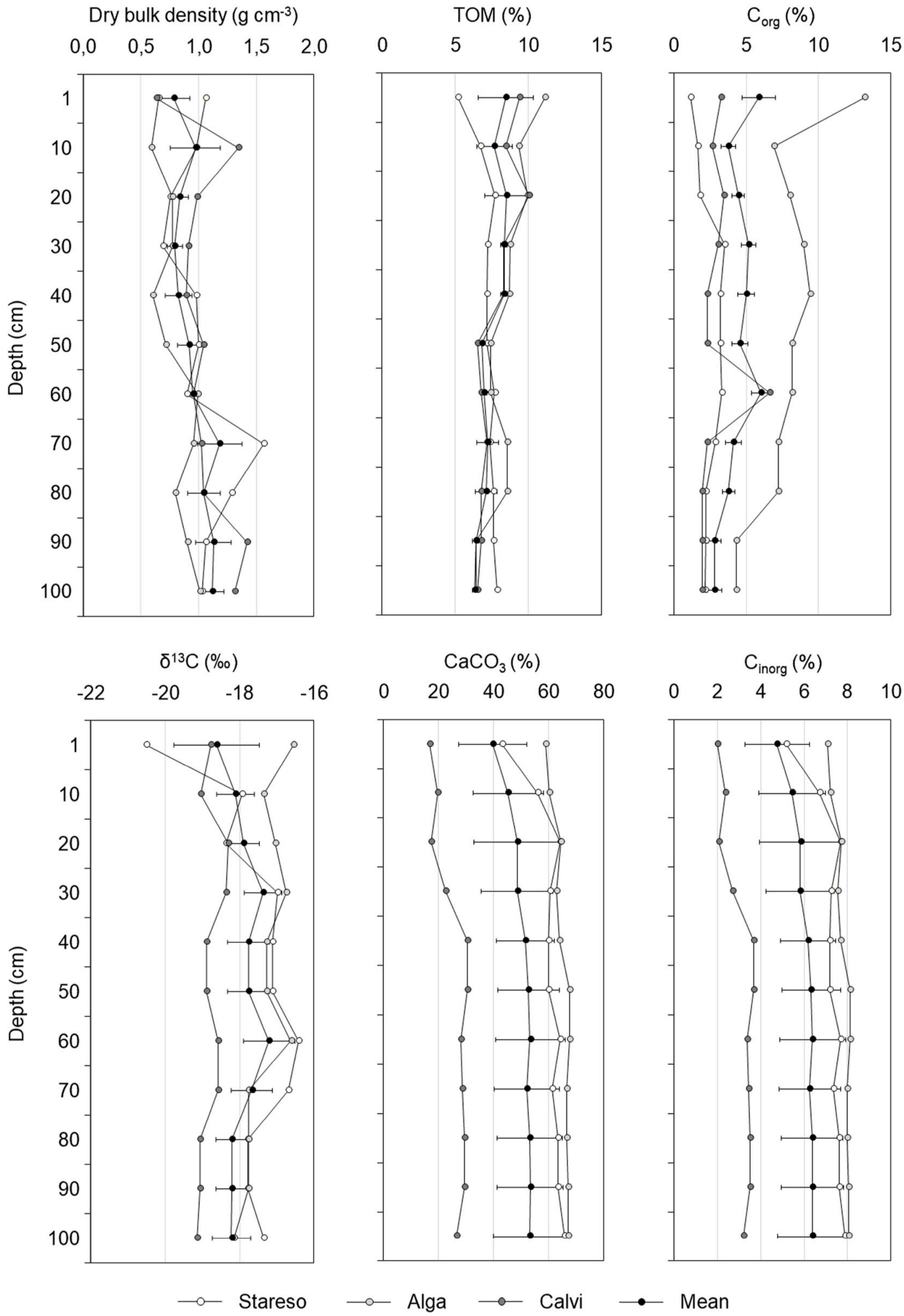

Fig. 9. Changes in the main parameters over the first 100 cm of *P. oceanica* matte cores investigated in this study. The contents in organic and inorganic carbon (% C_{org} and % C_{inorg}, respectively), total organic matter (%TOM), calcium carbonate (% $CaCO_3$) are expressed as percentage of the total sample dry weight (%).

0.3 ± 0.1 to 0.4 ± 0.3 mm yr^{-1} for the top 100 cm of the matte at 20 m depth) are similar to other values observed at the Corsican scale (0.7 ± 0.1 to 0.6 ± 0.2 mm yr^{-1}; Monnier et al., 2021b) or Mediterranean scale (Romero et al., 1994; Mateo et al., 2005; Serrano et al., 2012c; 2016). The high variability found in the sediment accretion rate suggests that high spatial and temporal changes occurred mainly due to the complex interplay of biotic and abiotic factors (*e.q.* meadow landscape and density, hydrodynamic energy, geomorphology) (Serrano et al., 2012c). In the case of the Calvi Bay, the most likely factors explaining the differences in accretion rates are variations in coastal sediment inputs (*e.q.* influence of watersheds) or exposure to marine currents along the coastline. The site of Stareso presents a chronostratigraphic age-depth

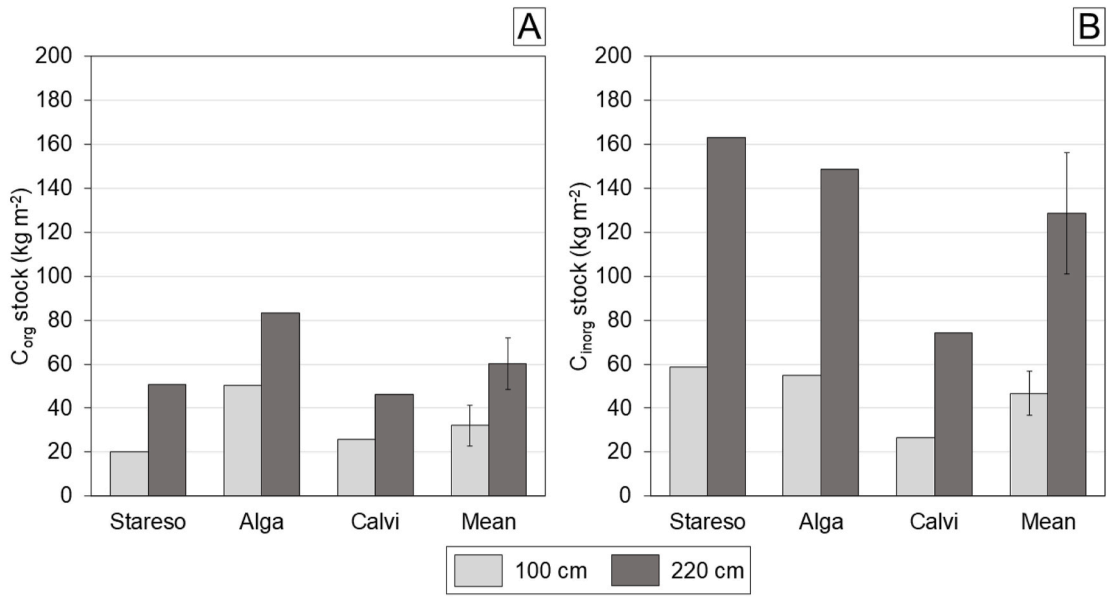

Fig. 10. Stocks of C_{org} (A) and C_{inorg} (B) determined in the top 100 cm (light grey) and 220 cm (dark grey) of *P. oceanica* matte deposits through the different stations (Stareso, Alga and Calvi). The mean represents the average value obtained from the three stations.

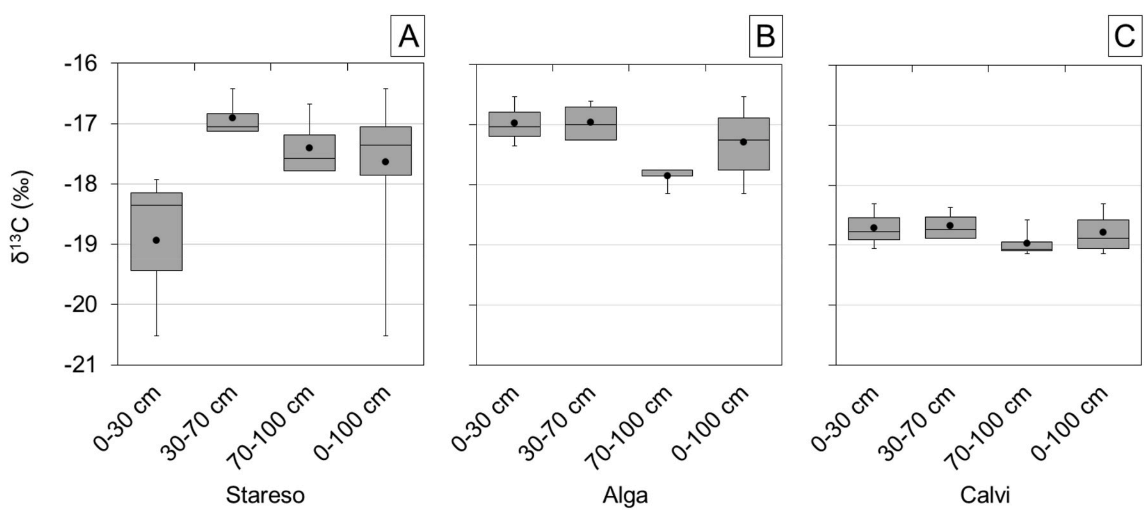

Fig. 11. Box plots of $\delta^{13}C$ values of the sedimentary organic carbon.

model very different from those of the Alga and Calvi stations (Table 3). Considering the top 100 cm, no significant difference was observed in accretion rate between the different stations. However, considering the first 30 cm of matte, the Stareso station exhibited a four-fold higher accretion rate than other ones (2.5 mm yr^{-1} and 0.6 mm yr^{-1}, respectively). Additionally, for the last 100 cal yr BP period, the accretion rate in Stareso station remains higher (2.15 mm yr^{-1}) than for Alga and Calvi stations (0.64 and 0.76 mm yr^{-1} respectively).

This difference could be explained by different factors: (i) by the geomorphology of *P. oceanica* meadows. The Stareso station is characterized by the presence of *P. oceanica* meadows growing mainly on rocks whereas at the Calvi stations meadows are settled on sandy substrates and the one in Alga is mixt. This hypothesis was controversial by different studies like Di Maida et al. (2013) in which the growth parameters (growth rate, leaf length and shoot surface) are lower in meadows on rock than on other substrates. The first reason is by the anchor pressure on the Alga Bay. For instance, in 2020, 693 boats were anchored on this small bay covered mainly by *P. oceanica* (Fullgrabe et al., 2022). The second reason is by the sedimentary contributions to the Calvi station which can lead to a higher turbidity and thus reduce the productivity and the horizontal growth of the meadow on this site.

From the previous studies, it appears that a large number of factors can potentially influence the accretion and the carbon stocks in seagrass meadows (Serrano et al., 2012c; Dahl et al., 2016; Serrano et al., 2016c). Here, the important variability found between nearby sites suggests that it is primordial to encompass in evaluations of carbon stocks the historical changes as well as environmental and biological variables that can explain the variability of accretion rates and carbon stocks (López-Sáez et al., 2009).

4.3. Carbon stocks

The results showed an important variability in the C_{org} and C_{inorg} stored in the *P. oceanica* meadows. However, C_{org} stocks (23.6 kg C_{org} m^{-2} to 58.9 kg C_{org} m^{-2}) were coherent with other studies at the Corsican scale (14.4–44.3 kg C_{org} m^{-2}; Monnier et al., 2022) and Mediterranean scale (4.7–75.5 kg C_{org} m^{-2}; Romero et al., 1994; Mateo et al., 2006; Serrano et al., 2012c; Piñeiro-Juncal et al., 2021). Stocks of C_{org}

show a consistent difference between the Stareso station and the two others (Calvi and Alga). The development of seagrass meadows and particularly *P. oceanica* could be influenced by the substrate on which it is settled (Mazarrasa et al., 2018; 2021). Seagrass meadows growing on rocky matrix are generally influenced by a higher exposure to hydrodynamic energy and a lower sediment particles deposition affecting the C_{org} accumulation in the seagrass sediments (Vacchi et al., 2016; Monnier 2020). At regional-scale, Monnier et al. (2022) showed that *P. oceanica* meadows settled on rocky matrix exhibited significantly lower C_{org} stocks compared to meadows growing on sandy substrate. These results appear to be consistent with the observations made in the Calvi Bay. The Stareso station, characterized by a *P. oceanica* meadows settled on a rocky substrate show two-fold lower C_{org} stock (20.2 kg C_{org} m^{-2}) than Alga and Calvi stations (38.1 ± 10.0 kg C_{org} m^{-2}) where *P. oceanica* grows on sandy substrate.

When compared with terrestrial ecosystems, the mean value of C_{org} within the first meter of soil obtained is higher than any land carbon storage such as boreal and polar vegetated soils (14.9 kg C_{org} m^{-2} and 11.8 kg C_{org} m^{-2}, respectively) or tropical wet and montane forests (6.1 kg C_{org} m^{-2} for both; Batjes et al., 2011). These results also confirm that *P. oceanica* stores more C_{org} than other seagrass species such as the plurispecific Australian meadows that have a storing capacity of 1.1–20.1 kg C_{org} m^{-2} (Lavery et al., 2013).

The changes in $\delta^{13}C$ values in *P. oceanica* mattes confirmed that both seagrass-derived (autochthonous sources) and non-seagrass-derived materials (allochthonous sources) were preserved in seagrass meadow sediments of the Calvi Bay (Gacia et al., 2002; Kennedy et al., 2010; Table S2). The lower average value of ^{13}C observed on the Calvi station may results from the higher deposition of allochthonous organic matter inputs coming from the estuary located at the eastern part of the Calvi beach sector (Fig. 2). Similar decrease in $\delta^{13}C$ signal of *P. oceanica* matte sediment has been observed near the river mouth on the eastern continental shelf of Corsica Island (Monnier et al., 2022).

The high variability in C_{inorg} stock estimated in this study (26.6–58.7 kg C_{inorg} m^{-2}) is coherent with evaluations from the Mediterranean region (Mazarrasa et al., 2015). However, the average C_{inorg} stocks found along the western coast exhibit higher values compared with estimations performed on the eastern coast of Corsica (24.5 ± 4.5 kg C_{inorg} m^{-2}; Monnier et al., 2022). The high C_{inorg} stocks found in Calvi Bay may be related to the presence of past biogenic carbonate production. The difference of accumulation of C_{inorg} may be explain because these two coastal ecosystems differ in terms of oceanographic conditions (sandy plains with depth not exceeding 500 m on east and coast frontal structure with significant depths on west coast) and environmental conditions (climate forcing, physical conditions, and nutrient availability) (Garrido et al., 2014). The eastern coast of Corsica is a sediment-starved slope, with little direct sediment supply from the adjacent continental shelf, littoral zone and continent. In contrast, the western flank is characterized by dominant current and turbiditic deposits (Miramontes et al., 2019).

4.4. Implication for coastal management

The present study constitutes one of the largest assessments of the carbon stored in the *P. oceanica* matte and the second one that took place in Corsica (Monnier 2020; Monnier et al., 2020; 2021, 2022). Beyond providing an estimation of the stocks of C_{org} and C_{inorg} in *P. oceanica* matte, this study stressed the importance of knowing the map of the matte thickness on an area of more than 20 km^2. This work underlines the possibility for environmental managers of Mediterranean coastal areas to assess the carbon stocks of seagrass meadows using this methodology. The high spatial heterogeneity of the matte thickness described by Monnier et al. (2021) can only be addressed through the use of accurate maps of benthic marine habitats (biocenosis and bottom types) as well as high-resolution seismic dataset of the below ground complex. Thanks to the emergence of lighter and more accurate acoustic equipment, the evaluation of the blue carbon stocks associated with the marine coastal habitats can be precisely undertaken. However, there is still the difficulty of realization of the cores which are an essential data for the interpretation of the acoustic data. This new insight in the hotspots of carbon storage should lead to more focused actions to protect key habitats such as the *P. oceanica* meadows to avoid their destruction and the release of carbon stored for thousands of years.

Author contribution

Michèle Leduc: Conceptualization, Methodology, Formal analysis, Investigation, Formal analysis, Data curation, Writing - Original Draft, Writing - Review & Editing, Visualization, Supervision, Project administration. **Arnaud Abadie:** Conceptualization, Methodology, Validation, Investigation, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing, Visualization. **Christophe Viala:** Investigation, Data curation. **Alban Bouchard:** Data curation. **Laura Iborra:** Formal analysis. **Quentin Fontaine:** Data curation. **Gilles Lepoint:** Data curation, Writing - Review & Editing. **Michel Marengo:** Writing - Review & Editing. **Gérard Pergent:** Conceptualization, Methodology, Validation, Resources, Writing - Review & Editing, Project administration, Funding acquisition. **Sylvie Gobert:** Writing - Review & Editing. **Pierre Lejeune:** Conceptualization, Methodology, Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition. **Briac Monnier:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing - Original Draft, Writing - Review & Editing, Visualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Leduc reports was provided by STARESO. Leduc reports a relationship with STARESO that includes: employment.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2022.105847.

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