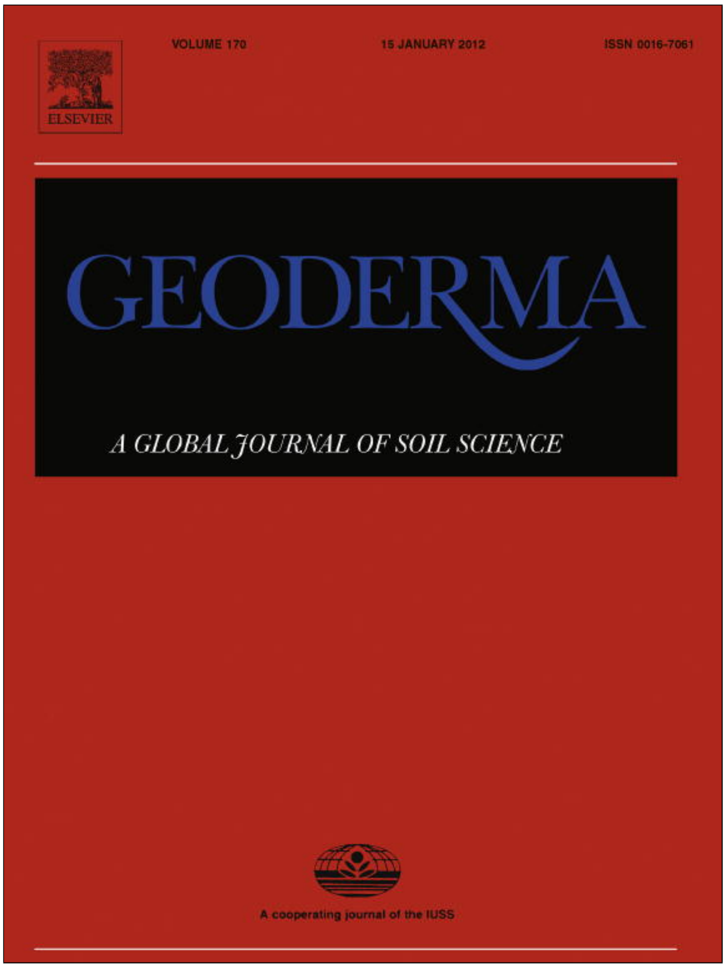

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Characterization of soils beneath a *Posidonia oceanica* meadow

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ABSTRACT

The study of a 475 cm core (spanning 4316 y BP) sampled in a *Posidonia oceanica* meadow (Portlligat Bay, NW Mediterranean) allowed us to make the first detailed description of the soil below this endemic seagrass. The sediments under *P. oceanica* (often referred to as mat or *matte*) are low density (average bulk density of 0.69 g DW cm^{-3}) marine soils mainly composed of siliciclastic (46%) and biogenic carbonated (46%) fine-grained sediments (particles <0.25 mm constitute more than 60% of the total inorganic particles). They are also composed to a lesser extent by coarse organic matter (5% of COM; >1 mm) and finer organic matter (3% of SOM; <1 mm). The mat is heterogeneous, and has a high total organic matter (TOM) content in the upper layers (average of 32% in the top 50 cm, after ca. 500 years of burial), after which the layers become increasingly dominated by inorganic fractions (ranging from 20 to 1% of TOM in 50–475 cm). The TOM content in the mat decreases exponentially at an overall rate of 0.0005 y^{-1}. *P. oceanica* sediments have been found to contain the highest areal stocks of TOM and organic C (194 kg DW TOM m^{-2} and 79 kg C_{org} m^{-2}, respectively) out of all seagrasses. The average C_{org} refractory-burial rates were estimated to be 21 g C_{org} m^{-2} y^{-1}. Carbon as carbonates accreted at a rate of 54 g C_{carb} m^{-2} y^{-1}. For the mat thickness studied, the two C fractions yielded a total stock that is among the highest ever recorded in terrestrial and marine soils (282 kg C_{TOT} m^{-2}). The mat was also found to trap large amounts of sediment (rate: 899 g DW m^{-2} y^{-1}; stock: 3342 kg DW m^{-2}), and in particular muddy (silt and clay) fractions (rate: 120 g DW m^{-2} y^{-1}; stock: 417 kg DW m^{-2}). The results obtained in this study provide sound additional proof of the valuable role *P. oceanica* plays in stabilizing coastal sediments and sequestering C, and also of its potential as a Holocene palaeorecord. The *P. oceanica* mats located at shallow depths (<2 m) can be tentatively classified as a Limnic Subaquatic Histosols (Calcaric, Eutric) (World Reference Base for Soil Resources, 2007).

1. Introduction

The *in situ* accumulation of large quantities of biogenic materials over millennia is of clear ecological relevance as these materials can act as palaeoclimatic records, sinks for biogenic elements and organic reservoirs, among others. Mangroves, tidal salt marshes, coral reefs and seagrass ecosystems are probably the best known examples in coastal areas (e.g. Laffoley and Grimsditch, 2009; Mateo et al., 1997), and peatlands and wetlands in terrestrial ecosystems (e.g. Chmura et al., 2003; Clymo, 1992).

Mangroves, seagrass meadows and tidal salt marshes each account for only around 1% of the dominant terrestrial habitats (i.e. forests, grasslands and deserts). The total C stock in these marine systems, however, is similar to that observed in many terrestrial systems (Laffoley and Grimsditch, 2009 and references therein). One remarkable difference between coastal marine habitats and terrestrial habitats is the capacity of the former for long-term C sequestration in sediments, which is due to their high primary productivity (Bertrand and Lallier-Vergès, 1991) and the extensive belowground detritic compartment that results from the very low decay rates under highly anoxic conditions (Canfield, 1994).

Posidonia oceanica is the most important and abundant seagrass in the Mediterranean Sea, where it forms extensive meadows from the surface down to 40 m water depth, covering around 25,000–50,000 km^2 (Pasqualini et al., 1998) and providing highly valuable ecosystem services (Green and Short, 2003). Previous studies have shown that *P. oceanica* sediments can bury large amounts of biogeochemical elements, such as organic C, carbonates, nutrients (Lo Iacono et al., 2008; Mateo et al., 1997; Romero et al., 1994) and metals (Serrano et al., 2011). They thus constitute a sink of key elements which has potential implications on a global scale. They are also known to hold the largest and oldest refractory C stocks among seagrasses, with residence times longer than 10,000 years (e.g. Mateo et al., 2006), which has important implications for the global C cycle (Duarte et al., 2010; Kennedy et al., 2010; Smith, 1981). However, although seagrass meadows could account for 15% of the ocean's total C storage, their role as a biogeochemical sink remains largely unexplored (Duarte et al., 2005; Laffoley and Grimsditch, 2009).

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Carbon stocks under *P. oceanica* meadows are deposited and form a highly organic, terraced structure known as mat (or "matte" in earlier descriptions by French authors; Boudouresque and Meinesz, 1982; Pérès and Picard, 1964), consisting of intertwined roots and rhizomes trapped in the inorganic sediment. The mat is the result of the balance between material accretion (detritus and sediment), decomposition and erosion (e.g. Mateo et al., 1997).

To our knowledge, Frost (1969), in a study for determining the chronological frame of a shipwreck buried below a 4 m high mat in Malta, was the first to use radiocarbon dating of a mat, obtaining the result of 1100 y BP. Further studies have revealed that *P. oceanica* remains can be found in the sediment as deep as 8 m and can be at least 5800 years old (Lo Iacono et al., 2008; Molinier and Picard, 1952; Picard, 1953). The vast majority of the mats that have been studied showed an excellent chronological arrangement, which suggests that the accretion rates, and thus the environmental stability, were considerably consistent (Mateo et al., 2010).

Significant research has focused on *P. oceanica* meadows in relation to plant ecology and palaeoecology (Buia et al., 1992; Mateo et al., 2010), floral and faunal communities (Mazzella et al., 1989) and hydrodynamics and sediment retention within the meadow (Gacia and Duarte, 2001). However, there are few studies on the substrate that supports the seagrass community. Some studies have analyzed *P. oceanica* sediments and determined the relationships between sediment distribution and *P. oceanica* seagrass (De Falco et al., 2000) and the sediment biochemistry (Holmer et al., 2003), but the information provided by previous studies is only for the top (i.e. 20 cm) sediment layers and there is still no detailed description of a long consistent mat sequence.

In this study we provide a detailed description of mat coring procedures and of the major constituents of a 475 cm continuous mat sequence. Direct estimates of the amount of C (C_{org} and C_{carb}) and sediments accumulated in the *P. oceanica* mat are also given.

2. Materials and methods

2.1. Sampling site

A 5.45 m long core of *P. oceanica* mat was sampled in Portlligat Bay (NW Mediterranean, Girona, Spain; Fig. 1) at 3 m water depth. Portlligat is a shallow bay (<10 m deep) connected to the sea through a 213 m opening to the NE. The seafloor is dominated by a consistent meadow (with some interspersed sandy bioclastic areas) that covers around 69% of the total area (94,315 m^2). The sampling site was chosen because it is part of a marine protected area and because it has a large *P. oceanica* meadow in a good state of preservation. Furthermore, the coring area is located at a distance of only 2 m from a *P. oceanica* barrier formation, which ensured that there would be a thick, well developed *P. oceanica* mat.

2.2. Mat coring

The core was sampled from a floating drilling platform firmly anchored with 4 ropes fixed to 1.5 m iron bars driven into the sediment. The corer consisted of a 150 cm long stainless steel pipe with an outer diameter of 105 mm, and an 88 mm (outer diameter) PVC pipe inside it. A 5 cm long removable coring head was attached to the pipe by means of a fast fitting system. This head was specially designed to penetrate and cut fibrous material and thus minimize core shortening (compression) and 'nail' effects during drilling.

The corer was pushed down from the platform into the sediment by attaching 1 m iron bars that connected the corer to a self-powered pneumatic hammer (Cobra, Atlas-Copco) that combined pneumatic percussion and rotation. The potential core size that can be sampled with this corer is 155 × 8.5 cm (length × diameter). The descent rate of the core was kept at about 25 cm min^{-1} to minimize core shortening. After drilling, the corer was pulled out by means of a manual crane fitted to the platform. The 5 bottom cm of the core were lodged directly in the coring head (i.e. not in the PVC pipe), and stored apart in separate containers. This operation was repeated three more times by driving the corer back into the hole made in the mat in the previous operation (assisted by SCUBA divers). The maximum depth that the corer reached in the sediment was recorded by measuring the length of the iron bar used.

The lengths of material recovered in the 4 coring operations (hereafter referred to as core Sections 1, 2, 3 and 4) were 123, 124, 134 and 143 cm, respectively, which makes a total core length of 524 cm, plus the 20 cm lodged directly in the coring head during the four coring operations. Cores were sealed at both ends, transported vertically the same day to the laboratory and stored at 5 °C before processing.

2.3. Laboratory procedures

Sections were cut longitudinally into two halves, and then one half of each section was cut into 1 cm slices. Each slice was weighed before and after oven-drying at 70 °C until constant weight (DW).

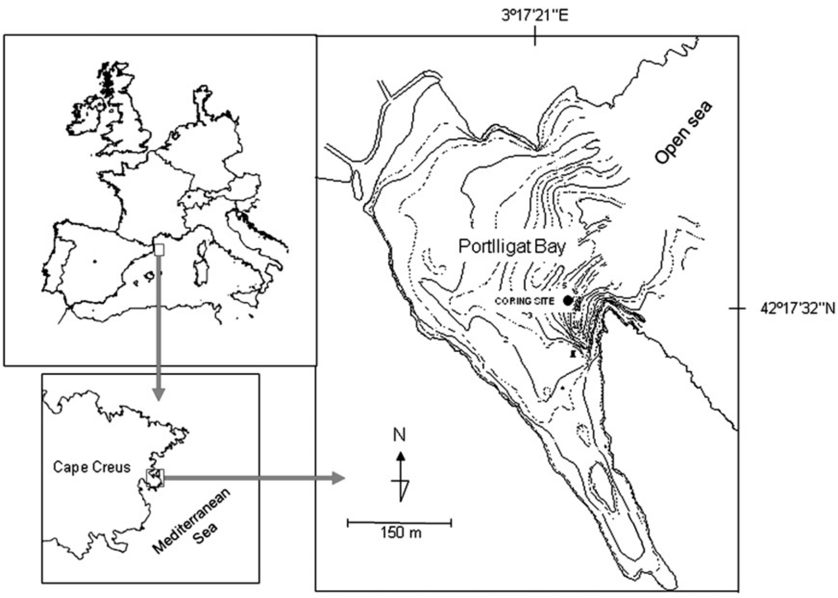

Fig. 1. Study site. Location of the study area at Portlligat Bay (NE Iberian Peninsula) and the drilling point in the *Posidonia oceanica* meadow.

Samples were subsequently sub-divided by quartering. The SOM (sediment organic matter <1 mm) and the total carbonate content ($CaCO_3$) were then measured in aliquots from about half of the slices (every second one). The SOM was determined by measuring the weight loss on ignition at 450 °C for 5 h of dry-sieved samples (<1 mm) The $CaCO_3$ was determined using a Scheibler calcimeter (Nelson, 1982). Five millilitres of 10% HCl were added to 0.4 g DW milled sediment and the volume of CO_2 evolved was recorded and compared to a standard of 0.2 g of pure carbonate (dry $CaCO_3$ powder, Baker Analyzed).

Raw sub-samples were re-suspended in seawater and wet-sieved (1 mm and 63 µm mesh) into two fractions: coarse (>1 mm) and fine (1 mm≥fine>63 µm). The coarse fraction was then re-suspended in seawater and sorted into organic (coarse organic matter, COM, >1 mm) and inorganic fractions. The COM was separated into sheath-, root- and rhizome-derived remains. The sum of SOM (<1 mm) and COM (>1 mm) was considered to be the total organic matter (TOM). All fractions were dried and weighed separately. The grain size was determined in 25–35 g DW sediment samples using a Retsch AS 200 analytical sieve shaker for 15 min after wet sieving (1 mm and 63 µm mesh) with distilled water and removing the COM. The sediment fraction smaller than 63 µm in diameter was determined by wet sieving according to the method of Holme and McIntyre (1971). No dispersants were used before the grain-size analysis because they are inappropriate for determining the transportability of sediment by flow (e.g. Slattery and Burt, 1997), and could lead to misleading ecological and geological interpretations. It should be kept in mind that this procedure underestimates the total amount of mud in the sediment. Sediments were classified as gravel (>2 mm), coarse sand (<2 mm and >0.5 mm), medium sand (<0.5 mm and >0.25 mm), fine sand (<0.25 mm and >0.063 mm) and mud (silt and clay, <0.063 mm), according to a scale adapted from Brown and McLachland (1990).

The elemental C composition of the *P. oceanica* sheaths was determined according to the gases that evolved from a single combustion using a Finnigan Delta S isotope ratio mass spectrometer 196 (Conflo II interface) at the Scientific-Technical Services of the University of Barcelona.

2.4. Radiocarbon dating

Nineteen samples of *P. oceanica* sheath remains were radiocarbon dated at the National Ocean Sciences AMS Facility (Woods Hole Oceanographic Institution, Woods Hole, MA) following standard procedures (Stoddart, 1969; Stuiver and Pollack, 1977; Table 1; Fig. 2). Sheaths were rinsed in ultrapure MQ water in order to remove fine sediment particles. They were inspected under a stereomicroscope for attached reworked materials, and dried at 60 °C to a constant weight before radiocarbon dating. All dates reported in this paper are expressed as radiocarbon dendrocalibrated years determined with the CALIB software v.4.4 (Stuiver et al., 1998).

2.5. Reconstruction of the chrono-stratigraphic sequence

The corer reached a maximum depth of 482 cm into the sediment during the four coring operations. Core compression and reworked material accounted for the difference between the total length of the cores recovered (545 cm) and the real length of the iron bar used (482 cm). Reworked material was observed in the upper parts of core sections II, III and IV. This material came from upper mat levels as the corer scraped the walls of the hole during successive coring operations. Fortunately, the reworked material could be easily identified by the naked eye because it appeared exceptionally regularly layered. Radiocarbon dating confirmed the observations and allowed a continuous chrono-stratigraphic sequence to be obtained as it clearly defined the reworked material in sections II, III and IV (21, 70 and 80 cm upper portions, respectively; Fig. 2). The increasing length of the reworked material was consistently related to the increasing distance that the corer travelled down into the sediment in successive operations.

Table 1
Details of radiocarbon dating of the *P. oceanica* sheath samples from the core. The accession laboratory sample number assigned by NOSAMS is indicated. The reservoir effect (RE) affecting the ages was estimated at 353 years. The ages labeled with an asterisk were not included in the time-stratigraphic framework (see text for further details).

Depth (cm)	NOSAMS #	Raw age (year BP)	Age error (+/−)	Corrected age (year BP-RE)
41	OS-29665	710	45	357
62	OS-29666	895	45	542
77	OS-29667	975	40	622
110	OS-29668	1430	40	1077
145	OS-29651	1600	45	1247
213	OS-44491	1710	25	1357*
255	OS-44492	2120	30	1767
287	OS-44493	2270	30	1917
307	OS-44494	2500	30	2147
326	OS-44497	2560	25	2207*
355	OS-44498	3130	25	2777
386	OS-44499	3320	30	2967
415	OS-44502	3500	35	3147
437	OS-44504	3850	30	3497

Compression of loose soils during coring is an inevitable phenomenon and is routinely corrected by distributing the spatial discordances proportionally between the expected and the observed sediment column layers (e.g. Glew et al., 2001), taking the top of the core and the maximum depth reached as references. In this study, the following negative exponential 'decompression' function was used:

$$Df = 336.02\mathrm{xexp}^{-0-0860p} \tag{1}$$

where *Df* is the decompression factor that needs to be subtracted from the observed position of a given layer of the core in order to determine its actual un-decompressed position, and *Op* is each of the observed positions. In this research, all the variables studied along the core were plotted against the corrected decompressed depths.

The marine reservoir effect due to the C dissolved in marine water was taken into account by considering the point of intersection of the fitted linear function and the x-axis in the uncorrected age *vs.* depth plot as the regionally-specific age offset (i.e. by subtracting 353 y from the raw laboratory radiocarbon ages). This correction is in good agreement with the reservoir effect determined for the Mediterranean Sea (390 ± 85 y; Siani et al., 2000) and fits the assumption that the age of the core top (living seagrass) is recent.

The ages corrected for the marine reservoir effect (excluding two inconsistent datings; Table 1) were used to produce an age-depth model with the Clam.R software (Blaauw, 2010). The best fit was obtained with a smooth-spline model, and is represented in Fig. 3. According to this model, accretion rates ranged from 0.7 to 2.7 mm y^{-1}, and resolution ranged from ~4 to ~15 y cm^{-1}. The core studied was 475 cm long and encompassed the last 4320 cal y BP.

2.6. Numerical procedures

The long-term accumulation rates (g DW m^{-2} y^{-1}) of the variables studied (inorganic sediments, mud, TOM, carbonates and C) were calculated by multiplying the average g DW m^{-2} cm^{-3} content in the 475 cm-thick mat by the average mat accretion rate (1.3 mm y^{-1}). The standing stocks per unit area (kg DW m^{-2}) were computed considering a mat thickness of 475 cm. It was assumed that the average C content in the *P. oceanica* sheaths along the mat (40.9%) is representative of the TOM.

All numerical procedures were performed using the statistics software package STATISTICA 7.1 (StatSoft, Okla.).

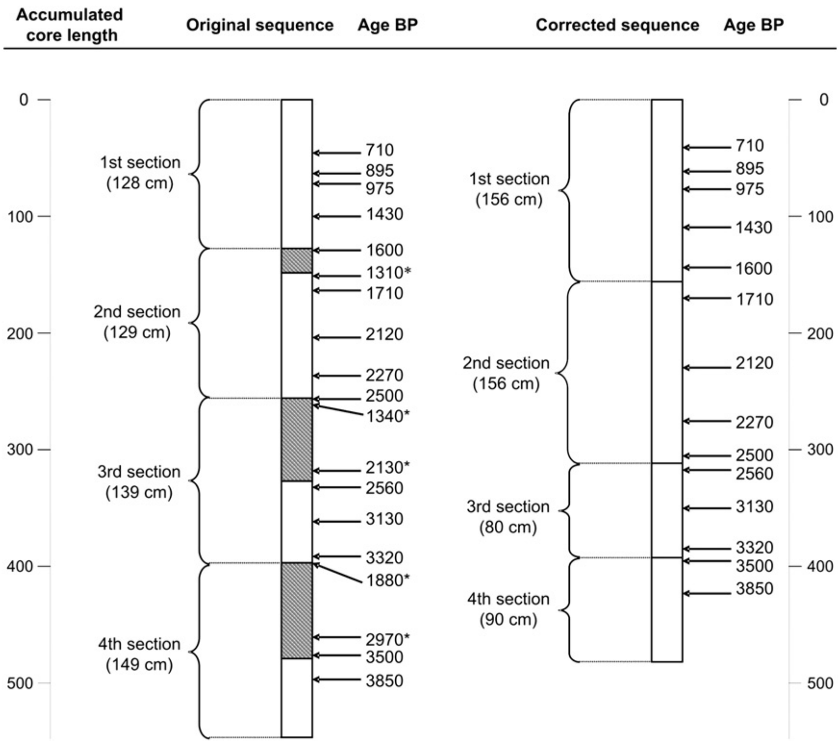

Fig. 2. Original chrono-stratigraphic sequence of the core sampled (left) and corrected for reworked material and core compression (right). The radiocarbon ages (y BP) labelled (*) in the original chrono-stratigraphic sequence define the reworked material in sections 2, 3 and 4 (dashed) which was scraped down by the corer in successive coring operations. The original and corrected core length of each core section is indicated in parentheses.

3. Results

3.1. Main features of the mat

The material recovered consisted of dark brown to grey peaty sediment that released an intense smell of sulphide. Stereomicroscope observations revealed abundant macro-remains of *P. oceanica* below-ground organs (roots, sheaths and rhizomes) embedded in a matrix of inorganic sediments, as well as abundant carbonate and siliceous remains of several phylum inhabiting *P. oceanica* meadows (i.e. Porifera, Cnidaria, Briozoa, Mollusca, Annelida, Arthropoda, Tardigrada, Foraminifera, Echinodermata and Rhodophyta). Fragments of exceptionally well-preserved *P. oceanica* rhizomes were found scattered all along the core (e.g. a 12 cm long rhizome dated at ca. 3800 y BP).

After corrections, we obtained a 475 cm core dating back to 4320 y BP, which had an average accretion rate and resolution of 1.3 mm y^{-1} and 9 y cm^{-1}, respectively (Fig. 3). The intervals between 1 and 122 cm (ca. last 1100 y BP), and 269 and 475 cm showed low accretion rates of 1.1 ± 0.2 and 0.9 ± 0.2 mm y^{-1}, respectively (Mean ± SD). Accretion rates significantly increased between 122 and 269 cm (2.2 ± 0.4 mm y^{-1}).

The mean bulk density was 0.69 g DW cm^{-3}, with a dry mass mainly composed by siliciclastic and carbonated sediments (46% in both cases), and to a lesser degree by TOM (8%; 5% COM and 3% SOM; Table 2). Bulk density values ranged from 0.05 to 1.40 g DW cm^{-3}, while the inorganic and carbonate contents ranged from 31 to 99% and from 11 to 64%, respectively. Fine sand was the most abundant grain-size fraction (49%), followed by medium sand, coarse sand, mud and gravel (16, 14, 13 and 8%, respectively; Table 2). Root remains were the most abundant COM fraction (61%), while the sheath and rhizome fragments accounted for 20% and 19%, respectively. The mean C content in sheath remains was 40.9% (Table 2).

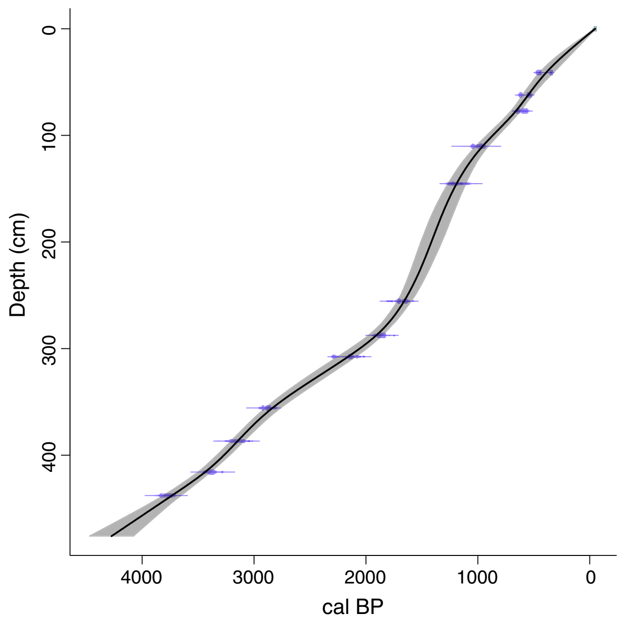

Fig. 3. Time-stratigraphic framework for the studied core. The solid line represents a best fit (a smooth-spline model) using 12 radiocarbon dates calibrated with the program "CALIB 4.4" and corrected for the reservoir effect.

3.2. Soil property changes with depth

The *P. oceanica* mat was not homogeneous and changed greatly with depth/age, mainly in relation to the decrease in TOM (Fig. 4). The mat started as a highly organic sediment (up to 69% in the top 14 cm, ca. 0–150 y BP) that rapidly turned into inorganic-dominated material (10% TOM at 52 cm, after ca. 500 y of burial). Thereafter, the TOM content slowly decreased towards the bottom of the core (average 5% TOM in 52–475 cm, 530–4320 y BP). Similarly, the upper section of the mat was a low compacted sediment (average bulk density 0.2 g DW cm^{-3}

Table 2
Descriptive statistics of the variables studied along the mat core. Mean ± S.E.M. (Standard Error of Mean); N (number of analyses); minimum and maximum values measured and the corresponding ages of the sample; coefficient of variation (CV); Pearson correlation coefficients (*r* value) between the variables studied and mat ages. Significance levels: $^{**}P<0.01$; $^{***}P\leq0.001$; NS, $P\geq0.05$. Bulk density, inorganic content, carbonate content, TOM, COM and SOM contents were expressed in dry weight percentage of total sample dry weight (%). Root, rhizome and sheath contents were expressed in dry weight percentage of TOM (%). C content in sheaths was expressed as dry weight percentage (%).

Variable	Mean	S.E.M.	N	Minimum	(y BP)	Maximum	(y BP)	CV (%)	y BP (*r*)
Bulk density (g dw cm^{-3})	0.69	0.02	306	0.05	25	1.40	2205	38	0.62***
Inorganic content (%)	92.18	0.76	175	31.41	163	99.24	3904	11	0.54***
Total carbonate (%)	45.74	0.83	175	11.22	751	64.42	1164	24	0.56***
TOM (%)	7.82	0.76	175	0.76	3904	68.59	163	128	0.54***
COM (%)	5.02	0.62	175	0.36	4287	54.08	163	164	0.47***
Root (%)	60.89	1.25	175	4.01	14	97.69	678	28	0.47***
Rhizome (%)	18.80	1.03	175	0.81	823	74.05	3904	73	0.56***
Sheath (%)	20.32	0.98	175	0.67	678	64.10	3481	65	NS
C in sheath (%)	40.86	0.19	175	33.88	926	46.55	549	6	0.25***
SOM (%)	2.80	0.17	175	0.26	2123	16.00	219	82	0.68***
Gravel content (%)	8.39	0.56	175	0.15	805	64.24	37	88	NS
Coarse sand content (%)	14.00	0.53	175	3.65	717	49.26	72	50	0.24**
Medium sand content (%)	15.86	0.28	175	5.20	37	26.24	1188	24	NS
Fine sand content (%)	48.99	1.09	175	7.76	72	78.86	709	30	0.53***
Mud content (%)	12.76	0.60	175	0.30	118	36.52	1632	62	0.64***

in the top 39 cm), which became increasingly denser until 150 cm (~1 g DW cm^{-3} after ca. 1300 years of burial). Thereafter, the mat density oscillated around an average value of 0.85 g DW cm^{-3} until the core bottom (Fig. 4).

The average carbonate content was lowest in the top 80 cm of the mat (28%) compared with the underlying levels (50%, 80–475 cm), but varied slightly over the mat sequence (coefficient of variation [CV] = 24%).

The vertical trends showed that density, inorganic and carbonate contents increased with depth (Table 2 and Fig. 4) and were positively correlated with each other (Table 3). However, the content of the organic matter fractions (TOM, COM and SOM) decreased with depth/age (Table 2), and was negatively correlated with density, inorganic and carbonate contents (Table 3).

Although TOM decreased exponentially with age, the preservation of the debris of the different plant parts (sheaths, roots, rhizomes) throughout the mat did not follow the same pattern (Fig. 4). The proportion of roots significantly decreased with age, while the rhizome content significantly increased and the sheath content did not follow any consistent trend (Table 2).

In general, the C concentration in sheath material remained rather constant throughout the sequence studied (CV = 6%; Table 2 and Fig. 4), and significant temporal variations were not observed.

The top 39 cm of the mat showed unique features, and was composed of 28% COM (5% sheath, 19% root and 3% rhizome), 8% SOM, 31% $CaCO_3$ and 33% non-carbonate sediments (Fig. 5a). It clearly differed from the underlying sections, which were composed on average of 4% COM, 2% SOM, 47% $CaCO_3$ and 47% non-carbonate sediments (Fig. 5b). In addition, the top 39 cm contained a higher amount of coarser sediments (18% gravel and 21% coarse sand) and a lower mud content (2%) in comparison with deeper mat layers (39–475 cm, 421–4320 y BP), which had 8%, 13% and 14% gravel, coarse sand and mud, respectively (Fig. 6).

The coarse sand and mud fractions significantly increased from the top to the bottom mat layers, fine sand significantly decreased, and gravel and medium sand did not follow any consistent trend (Table 2; Fig. 6). The coarser grain fractions (gravel and coarse sand) were positively correlated with all organic fractions, with the exception of coarse sand and SOM (Table 3). In addition, higher bulk density and inorganic and $CaCO_3$ contents were associated with mat levels with high medium sand and mud contents, and low fine-sand contents (Table 3).

3.3. Accumulation rates and stocks

The long-term accumulation rates of organic matter were estimated in 31 g DW COM m^{-2} y^{-1} and 21 g DW SOM m^{-2} y^{-1} (Table 4). The 475 cm of mat studied contained an average of 194 kg DW TOM m^{-2} (115 kg DW COM m^{-2} and 79 kg DW SOM m^{-2}; Table 4; Fig. 7a).

Total and muddy sediments accumulated at an overall rate of 899 and 120 g DW m^{-2} y^{-1} respectively, of which 453 g DW m^{-2} y^{-1} were carbonates (Table 4; Fig. 7b). The standing stock per unit area of inorganic sediments and mud in the total thickness studied was 3342 and 417 kg DW m^{-2} respectively, with a specific content of 691 kg DW m^{-3} of sediments and 92 kg DW m^{-3} of mud (Table 4). The stock of $CaCO_3$ was 1696 kg DW m^{-2}, with an average specific content of 348 kg DW m^{-3} (Fig. 7b).

4. Discussion

This study provides the first thorough description of the major constituents of a long continuous *P. oceanica* mat sequence. The radiocarbon dating of this 475 cm core revealed a highly consistent temporal accumulation with an average resolution of ~8 y cm^{-1}, encompassing the Subatlantic and the Subboreal Holocene. The TOM content observed is the highest recorded for seagrasses so far, and for any other known marine sediment, with the probable exception of the sediment under mangroves. Direct quantification (i.e. not based on accumulation models) confirmed a very high C content (C_{org} and C_{carb}), as well as small-sized sediment fractions. All these findings are coherent and reinforce the known role of *P. oceanica* as a unique sink of C and fine-grained sediments, and as a marine coastal record for the Late Holocene in the Mediterranean Sea.

4.1. Mat coring

The coring method used proved to be efficient for sampling cores of up to 5 m long in shallow meadows. However, the maximum thickness was limited by the floating capacity of the rig, which was exceeded when we attempted to obtain a fifth mat core due to the total weight of the iron bars, the pipe, the mat material and the friction. Another limitation concerned preventing the hole made in the sediment from collapsing and being filled in with mat debris from upper layers in successive coring operations. Although it was possible to discriminate between displaced and *in situ* materials due to differences in texture, expensive radiocarbon dating was needed for confirmation.

In addition, even though the most efficient practices for minimizing core compression were used (i.e. specially designed cutting edge, coring at a low descent rate and use of rotation), the overall degree of core shortening was high (22%), although within the expected range (up to 30%; Morton and White, 1997). Therefore, other coring techniques should be explored. The results obtained in this study and in Lo Iacono et al. (2008) show that vertical coring of the mat in the meadow is

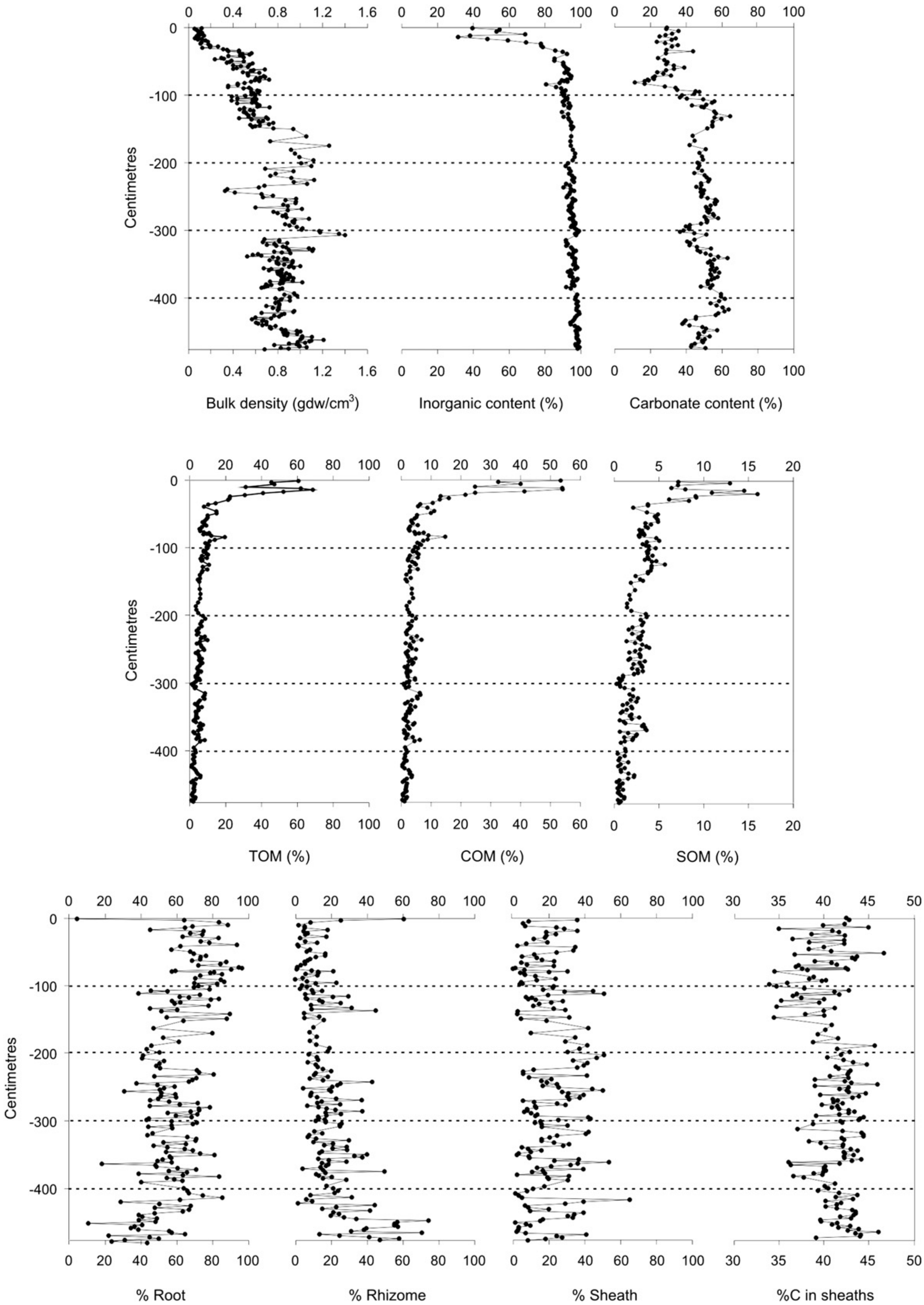

Fig. 4. Changes in the main components along the *P. oceanica* mat core from Portlligat. Inorganic content, carbonate content, TOM, COM and SOM contents are expressed as percentage of the total sample dry weight (%). Root, rhizome and sheath contents are expressed as the percentage of TOM (%). The C content in sheaths is expressed as percentage of dry weight.

preferable to sampling naturally eroded mat walls. This last sampling method has occasionally led to chrono-stratigraphic incoherencies (Mateo et al., 1997 and *unpublished results*), which were probably due to erosion and re-deposition phenomena and/or contamination by organic matter from living organisms.

4.2. The main features of the mat

The top 20 cm of the mat contained high amounts of TOM (51% on average), in agreement with previous studies (De Grissac and Boudouresque, 1985; Harmelin, 1964; Nesteroff, 1965). The TOM content

Table 3
Pearson correlation coefficients between the variables studied along the mat core. Bulk density, inorganic content, carbonate content, TOM, COM and SOM contents were measured in dry weight percentage of total sample dry weight (%). Root, rhizome and sheath contents were measured in dry weight percentage of TOM (%). C content in sheaths was measured as dry weight percentage (%). Levels of significance: *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$; NS, $P \geq 0.05$; Significant correlations in bold (*r* value).

	Density	Inorganic	Gravel	Coarse sand	Medium sand	Fine sand	Mud	Carbonates	TOM	COM	SOM
Density		**0.68**	0.10	**0.16**	**0.24**	**0.29**	**0.37**	**0.49**	**0.68**	**0.63**	**0.71**
Inorganic	***		**0.33**	**0.21**	**0.19**	0.01	**0.43**	**0.49**	-	**0.99**	**0.83**
Gravel	NS	***		**0.45**	**0.46**	**0.60**	0.02	0.04	**0.33**	**0.35**	**0.18**
Coarse sand	*	**	***		0.13	**0.79**	**0.20**	0.09	**0.21**	**0.28**	0.07
Medium sand	**	*	***	NS		0.10	0.10	**0.52**	**0.19**	**0.22**	0.07
Fine sand	***	NS	***	***	NS		**0.61**	**0.40**	0.01	0.06	**0.26**
Mud	***	***	NS	**	NS	***		**0.44**	**0.43**	**0.37**	**0.54**
Carbonates	***	***	NS	NS	***	***	***		**0.49**	**0.47**	**0.45**
TOM	***	–	***	**	*	NS	***	***		**0.99**	**0.83**
COM	***	***	***	***	**	NS	***	***	***		**0.73**
SOM	***	***	*	NS	NS	**	***	***	***	***	

along the core ranged between 1 and 69%, which is much higher than the TOM content in bare sandy surface sediments (e.g. 1—3% in subtidal sandy sediments of the Ligurian Sea, Fabiano et al., 1995) and shallow sandy bottoms near *P. oceanica* meadows (up to 4%; De Falco et al., 2000; Gobert et al., 2003).

The long-term accumulation rate of TOM was estimated at 52 g DW m^{-2} y^{-1} in agreement with previous studies on *P. oceanica* mat deposits (27—256 g DW TOM m^{-2} y^{-1}; Table 5). The average TOM content is the largest recorded among seagrasses and other known Mediterranean ecosystems (both marine and terrestrial). There is remarkably little information on organic accretion rates and stocks in other seagrass species or other marine vegetation in the literature. The few studies available (e.g. Duarte et al., 1998; Lipkin, 1979) cannot be directly compared with the present work because they only consider the top layers of the mat. In our view, this gap constitutes one of the main limitations for adequately assessing the role of coastal vegetation around the world as long-term C sinks.

The TOM content in the mat decreased exponentially at an overall rate of 0.0005 y^{-1} ($TOM = 15.087e^{0.0005x}$, $R^2 = 0.61$). The low turnover rates of the TOM in the mat are a consequence of the refractory nature of *P. oceanica* detritus (e.g. belowground organs have a high lignin content; Klap et al., 2000) and the anoxic conditions in the mat (anaerobiosis occurs below the first few centimetres of sediment; Mateo et al., 2006). The faster TOM decay rates during the first ca. 400 y after burial (1–39 cm) result from an initial rapid decomposition of the more labile organic compounds. After this period, *P. oceanica* remains that are rich in structural carbohydrates and highly refractory molecules continue to decompose at very slow rates (e.g. Mateo et al., 2006; Pedersen et al., 2011). Leaf blade detritus, however, does not accumulate because it decomposes within the first year after production (e.g. Mateo and Romero, 1996). Changes in the TOM and inorganic fractions along the core are difficult to interpret as they are a combination of changes in the ecosystem productivity, decomposition rates of the plant organs, mat accretion rates and terrestrial inputs.

Both the production and living biomass of *P. oceanica* rhizomes (including sheaths) are ~8 times higher than those of the roots (Mateo and Romero, 1996). In the mat, however, root detritus was up to 3 times more abundant than the other two fractions, which suggests that the different fractions have very different susceptibilities to decomposition. Since the preservation conditions within the sediment were the same for all fractions, differential tissue composition may explain the differential decay. This hypothesis is consistent with the C/N ratios in the various organs: 86, 75 and 59 for roots, sheaths and rhizomes, respectively (Mateo and Romero, 1996).

It has often been reported that the seagrass-derived organic matter is not always the dominant organic fraction in superficial seagrass sediments, but rather makes up around 51% (25–62%) of the total carbon pool of seagrass sediments (Kennedy et al., 2010; Mateo et al., 2006). However, this is not likely to be the case in the upper layers of *P. oceanica* mat sediments (almost 72% of TOM was coarse plant debris in the top 52 cm). In the lower parts, a dominance of the more recalcitrant seagrass-derived material would also be expected because the more labile algal-derived fractions may have been completely recycled.

Previous studies reported average bulk density values in 1 to 4 m thick *P. oceanica* mats ranging from 0.2 to 1.3 g DW cm^{-3} (Table 5), which is within the range of values reported in this study. The bulk density of the top 39 cm of the mat was particularly low owing to the high TOM content (average density ± SEM = 0.19 ± 0.03 g DW cm^{-3}), and comparable to that of peat (0.12–0.22 g DW cm^{-3}; Bellamy and Rieley, 1967; Tallis and Switsur, 1973).

The average $CaCO_3$ content (46%) fell within the range of 35% to 98% reported for other meadows in the Mediterranean Sea (e.g. Boudouresque and De Grissac, 1983; De Falco et al., 2000, 2003). Thus, the calcifying organisms (flora and fauna) inhabiting seagrass meadows

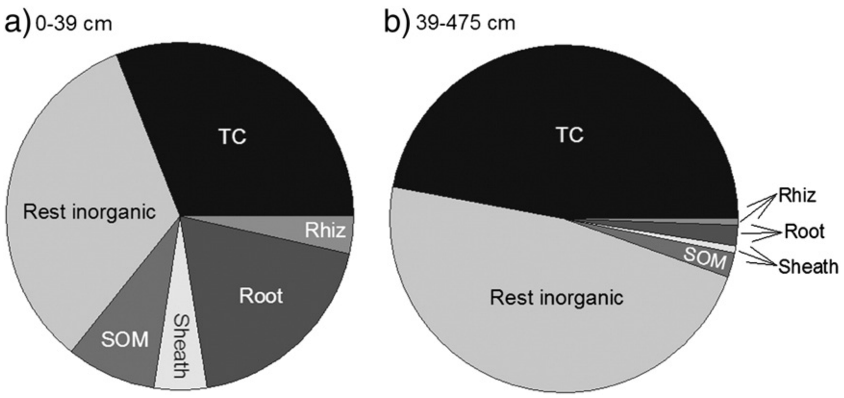

Fig. 5. Average composition in carbonates ($CaCO_3$), non-carbonate inorganic sediments (inorganic remains), coarse organic matter fractions >1 mm ("rhiz", rhizome, root and sheath) and fine organic matter (<1 mm, SOM) of the top 39 cm (a) and 39–475 cm (b) in the *P. oceanica* mat from Portlligat Bay.

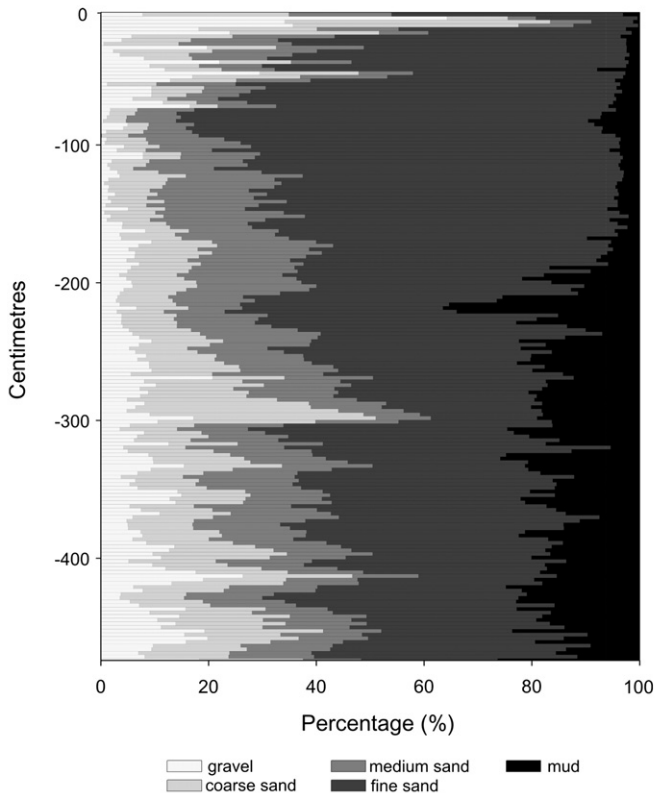

Fig. 6. Changes in the sediment grain-size fractions along a 475 cm-thick *P. oceanica* mat: gravel (>2 mm), coarse sand (<2 mm and >0.5 mm), medium sand (<0.5 mm and >0.25 mm), fine sand (<0.25 mm and >0.063 mm), and mud (<0.063 mm).

greatly increase the $CaCO_3$ sediment content (e.g. 3–7% of $CaCO_3$ in unvegetated sediments; De Falco et al., 2003).

It has been reported that superficial *P. oceanica* mat sediments from other Mediterranean bays are dominated by medium sands, muddy sands or coarse sands (De Falco et al., 2000, 2003; Gobert et al., 2003; Papadimitriou et al., 2005). The long sequence studied here, however, showed that below 20 cm, fine-grained sediments (particles <0.25 mm) constituted more than 60% of the total inorganic particles.

The positive correlations between carbonate content and both the medium sand and mud fractions suggest that many of the calcifying organisms that inhabited *P. oceanica* meadows were meiofauna (<0.5 mm). However, the presence of many macrofauna fragments with sizes lower than 0.5 mm was also noted, and therefore further studies are needed to accurately determine the contributors to the carbonate pool in the mat.

Previous studies on *Zostera* spp. suggest that the current distribution of submerged aquatic vegetation within an area is strongly influenced by the physical and chemical subaqueous soil characteristics (e.g. water depth, slope, landscape shape, depositional environment, texture and salinity), and therefore understanding the distribution of these soils and the associated characteristics would be valuable for coastal management (Bradley and Stolt, 2003, 2006). The subaqueous landscape/soil relationships in *P. oceanica* meadows are probably more complex than in other subaqueous environments because *P. oceanica* meadows are considered ecosystem engineers since they (i) modify the hydrodynamic energy (i.e. enhancing sedimentation and reducing resuspension; Gacia and Duarte, 2001), (ii) host large amounts of calcifying organisms (around 50–96% of soils are biogenic carbonates), (iii) modify the sea bottom bathymetry due to plant growth and soil elevation (e.g. >1 mm y^{-1}; Lo Iacono et al., 2008), (iv) create a complex structure with water circulation channels and interchannels (Boudouresque and Meinesz, 1982), and (v) occupy large extensions (particularly in the past). Once *P. oceanica* became established in the bay 5000 years ago the soils were completely modified by its presence (increased soil organic matter, mud and $CaCO_3$ content). The main goal of this study was to provide the first detailed description of a long, continuous core of *P. oceanica* mat and establish a basis for further studies of the subaqueous landscape/soil relationships in *P. oceanica*-dominated ecosystems. For this last aim, surveys to obtain information on large- and local-scale variability of seagrass soils need to be carried out.

4.3. Classification of *P. oceanica* soils

The sediments beneath *P. oceanica* meadows meet all the requirements for being considered a soil. They are altered by the interactions of climate, relief and living organisms over time and support rooted plants (Soil Survey Staff, 2010; WRB, 2007). In the last century pedologists already considered subaqueous sediments as soil, and currently subaqueous soils are those which occur from the intertidal zone to a depth that allows the growth of rooted plants (typically less than about 2.5 m) in coastal ecosystems (Soil Survey Staff, 2010; WRB, 2007). The shallow phases of the *P. oceanica* mats can be classified as a Limnic Subaquatic Histosols (Calcaric, Eutric) (WRB, 2007), although the WRB (2007) does not consider sub-aquatic material at depths greater than 2 m to be soils. Mat sediments have a >10 cm-thick surface histic horizon that starts at the soil surface and consists of poorly aerated carbon-rich organic material that is always saturated with water. Both organic and mineral materials are deposited by precipitation or through the action of aquatic organisms.

The soil described can only be representative of shallow *P. oceanica* meadows (1–5 m depth) located on continental shores, because *P. oceanica* meadows show a wide variability in the bathymetric distribution and differ greatly among continental and island shores (e.g. meadow density and cover). That only one pedon was observed limits the description of the type of soil, and further research would be needed for a more robust characterization of seagrass subaqueous soils.

Table 4
Estimates of long-term accumulation rates (g m^{-2} y^{-1} in dry weight [DW]) and total stocks (kg DW m^{-3} and kg DW m^{-2}) of inorganic sediments, mud sediments (<63 μm), carbonates ($CaCO_3$) and organic matter (COM, SOM and TOM) in the 475 cm *P. oceanica* mat core (top). Long-term C accumulation rates and total stocks of carbonates and organic matter (bottom). COM, coarse organic matter (>1 mm); SOM, fine sediment organic matter (<1 mm); TOM, total organic matter. Mean ± Standard Error.

DW/C	Compartment		Long-term rate of accumulation g m^{-2} y^{-1}	Standing stock kg m^{-3}	Standing stock kg m^{-2}
DW	Inorganic sediments		898.6 ± 26.3	691.2 ± 20.2	3342
DW	Mud (<63 μm)		120.0 ± 6.4	92.3 ± 4.9	417
DW	$CaCO_3$		452.9 ± 15.5	347.8 ± 10.0	1696
DW	Organic matter	COM	30.6 ± 1.3	23.6 ± 1.0	115
		SOM	21.2 ± 0.8	16.3 ± 0.6	79
		TOM	51.8 ± 1.7	39.9 ± 1.3	194
C	$CaCO_3$		54.3 ± 1.9	41.7 ± 1.2	203
C		COM	12.5 ± 0.5	9.6 ± 0.4	47
	Organic matter	SOM	8.7 ± 0.3	6.7 ± 0.3	32
		TOM	21.2 ± 0.7	16.3 ± 0.5	79
C	Total		75.5	58.0	283

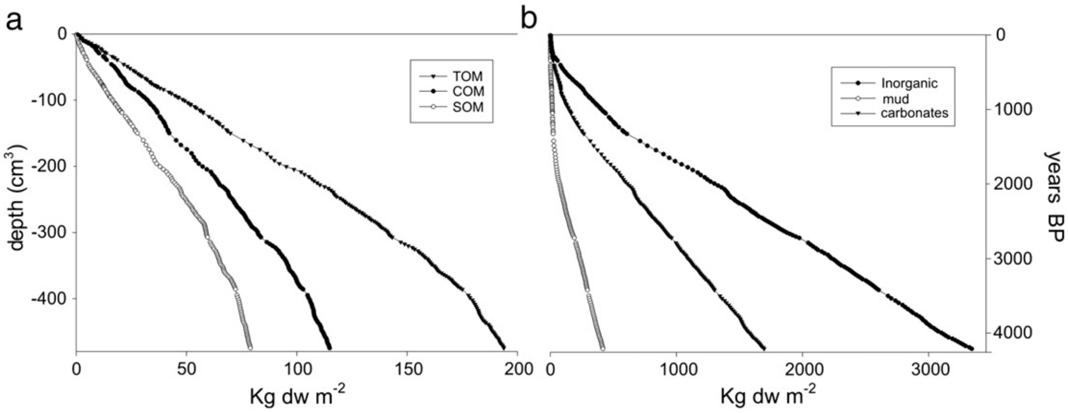

Fig. 7. a) Cumulative mass (kg DW m^{-2}) of organic matter (COM, SOM and TOM) in the 475 cm-thick *P. oceanica* mat. b) Cumulative mass (kg DW m^{-2}) of inorganic sediments, mud and carbonates along a 475 cm *P. oceanica* mat core.

4.4. Mat accretion rates

The vertical accretion rate of the mat is essentially the result of the balance between plant production, sedimentation, burial and erosion. The average mat accretion rate measured in Portlligat Bay (1.3 mm y^{-1}) is within the range of previously reported rates (0.6–10 mm y^{-1}; Table 5). Molinier and Picard (1952) reported the highest mat accretion rate for a mat in Port-Cros (France) to be 10 mm y^{-1}. However, it is quite likely that this rate is overestimated because of the rough, indirect method used, which was based on historical isobath changes and not on direct dating techniques. The accretion rates measured in *P. oceanica* mats agree with similar findings for sediments of *Posidonia australis*, which had accretion rates of 1–2.7 mm y^{-1} (Belperio et al., 1984).

The remarkable variability found in the mat accretion rates over the period reconstructed, and between nearby sites at Portlligat (average 1.3 mm y^{-1} *versus* 4.1 mm y^{-1} only 200 m away; this study and Mateo et al., 1997, respectively) suggests that there is high environmental patchiness and much interplay between multiple factors (e.g. meadow cover and density, hydrodynamic energy and sedimentation patterns, changes in productivity, etc.). Future studies should focus on understanding the mechanisms for spatial and temporal changes in mat accretion rates.

4.5. Implications of the mat as a palaeoecological record and in coastal biogeochemical cycles

The *P. oceanica* mat provides a new way of studying the historical changes in key environmental and biological variables during the Holocene in Mediterranean coastal areas (López-Sáez et al., 2009; Mateo et al., 2010; Serrano et al., 2011). Mat deposits meet the main requirements for ensuring reliable palaeo-reconstructions because they are chronologically consistent and have an appropriate resolution (1–17 y cm^{-1}; Table 5). The presence of abundant and very well-preserved remains of marine and terrestrial species in the mat opens exciting possibilities for reconstruction studies.

Based on an average organic C content in the mat of 40.9% (Table 2), the annual refractory accumulation and the stock of C_{org} for the mat thickness studied in Portlligat was estimated at 21 g C m^{-2} y^{-1} and 79 kg C m^{-2}, respectively (Table 4). These values are in the range of previous observations (9–112 g C_{org} m^{-2} y^{-1}, 40–160 kg C_{org} m^{-2}; Mateo et al., 1997, 2006; Romero et al., 1994), and confirm that the standing C_{org} stock per unit area in the *P. oceanica* mat is the highest ever recorded in marine ecosystems (Laffoley and Grimsditch, 2009 and references therein). Accretion rates for mangroves have been reported in a number of studies, with values between 90 and 400 g C_{org} m^{-2} y^{-1} (e.g. Bouillon

Table 5
Review of the available data on Mediterranean *P. oceanica* mats reported by other authors. The number of mat sequences sampled in exposed mat walls and their thickness, and the layers sampled in each case are indicated. NR (Data not reported).

Location	Num. of mat profiles	Layers sampled	Thickness cm	Depth m	Accretion mm y^{-1}	Resolution y cm^{-1}	Bulk density g dw cm^{-3}	COM accumul g dw m^{-2} y^{-1}
Port-Cros Is.–Bagaud (France)[a,b]	–	–	–	–	10.0	1.0	NR	NR
Antibes region (France)[c]	–	–	–	–	0.6–1.0	10–16.6	NR	NR
Giens (France)[d,e]	–	–	–	–	1.0–1.5	6.7–10.0	NR	NR
Port-Cros Is.–Portman (France)[f]	1	4	55	NR	1.0	10.0	NR	NR
Cala Culip (Spain)[g]	1	9	160	4.0–5.6	2.3	4.3	0.45	26.8
Portlligat S. Antoni I (Spain)[h]	3	3	135	3.0–4.4	4.1	2.4	0.43	178.0
El Campello (Spain)[h]	3	5	200	3.0–5.0	2.0	5.0	1.28	255.8
Tabarca Is. South (Spain)[h]	3	4	170	5.0–6.7	1.9	5.3	1.25	236.9
Ischia (Italy)[h]	1	5	320	10.0–13.2	1.7	5.9	0.50	84.2
Tabarca Is. North (Spain)[h]	1	3	100	1.5–2.5	1.1	9.1	1.31	143.6
Medes Is. (Spain)[h]	1	13	400	14.0–18.0	0.8	12.5	0.39	30.8
Villajoyosa (Spain)[i]	1	3	190	6.9–8.8	1.9	5.3	0.19	35.3
Portlligat Vailet Point (Spain)[j]	1	177	482	3.0–7.8	1.3	9.1	0.69	30.6

[a] Molinier and Picard (1952).
[b] Picard (1953).
[c] Nesteroff (1965).
[d] Maggi et al. (1997).
[e] Tchernia et al. (1978).
[f] Boudouresque et al. (1980).
[g] Romero et al. (1994).
[h] Mateo et al. (1997).
[i] Mateo et al. (2005).
[j] This study.

et al., 2008; Duarte et al., 2005; McKee, 2010; Twilley et al., 1992), and the total refractory stocks are potentially large (depths of mangrove sediment varied from <1 m to over 10 m; McKee, 2010); however, to our knowledge, there are currently no estimates. The standing C_{org} stock in the mat is higher than that in soils of tropical, temperate and boreal forests (9–34 kg C_{org} m^{-2}), tundra (13 kg C_{org} m^{-2}) and wetlands (73 kg C_{org} m^{-2}; Laffoley and Grimsditch, 2009 and references therein), and lower than in peats (120 kg C_{org} m^{-2}; Warner et al., 1993).

The studied meadow also accretes 54 g C m^{-2} y^{-1} in the form of carbonates, reaching a stock estimated at 203 kg C_{carb} m^{-2} after 4320 y of mat formation. The C_{carb} accumulation rates in Portlligat are similar to the only other available estimate for a *P. oceanica* meadow (Sardinia, 47–138 g C_{carb} m^{-2} y^{-1}; De Falco et al., 2008). These results confirm that these rates are among the highest reported for seagrass ecosystems (2–60 g C_{carb} m^{-2} y^{-1}; Gacia et al., 2003; Land, 1970; Walker and Woelkerling, 1988) and other Mediterranean coastal benthic ecosystems (i.e. algal communities and maerl beds; 25–56 g C_{carb} m^{-2} y^{-1}) and are much higher than in bare sediments (0.065 g C_{carb} m^{-2} y^{-1}; Canals and Ballesteros, 1997). While this C_{carb} represents a very important C stock, it has been shown that calcification represents a global CO_2 source to the atmosphere (Smith and Gattuso, 2009), and therefore *P. oceanica* meadows could represent a significant net CO_2 source (Mateo and Serrano, 2012).

The standing stock of C_{TOT} on a unit area basis in *P. oceanica* meadows (282 kg C m^{-2} for the mat thickness studied) is probably one of the highest ever reported so far, both for terrestrial and marine soils. Preliminary estimates based on the results obtained in this study suggest a stock of $7–14\times10^{15}$ g C_{TOT} in the Mediterranean Sea ($2–4\times10^{15}$ g C_{org} and $5–10\times10^{15}$ g C_{carb}; assuming that *P. oceanica* covers 25,000–50,000 km^2; Pasqualini et al., 1998). The C stock in *P. oceanica* soils is relevant when compared with the global C stocks for wetlands (225×10^{15} g C; Laffoley and Grimsditch, 2009), peat (450×10^{15} g C; Warner et al., 1993) and coral reefs ($100–400\times10^{15}$ g C, for the upper 1–4 m of reefs; Kinsey, 1983; Smith, 1978; Stoddart, 1969). However, it is important to note that the above comparisons are dependent on the sediment layer studied and on the estimated total area occupied by the ecosystem, two key parameters that are still far from being adequately addressed.

The grain-size analysis of mat sediments allowed the average content of the total sediments and the mud fraction to be estimated as 691 and 92 kg DW m^{-3}, respectively (Table 4). To the best of our knowledge, De Falco et al. (2000) are the only authors that have reported similar estimates (160–470 kg DW m^{-3} of sediment and 30–90 kg DW m^{-3} of mud), but their estimates were only based on the top 10 cm of the mat (organic-enriched). The results obtained in this study show that the top 20 cm of the mat are mud-depleted (~2%), probably because hydrodynamic forces can re-suspend the muddy sediments from the top of the mat, and/or the network of entire rhizomes and roots in these top layers may act as a sieve, concentrating the coarse-grained sediments and allowing fine sediments to sink down to deeper mat levels. Considering all of the above, it seems that the only available estimates (those by De Falco et al., 2000) are probably at the lower end of the range of the potential sediment content in *P. oceanica* meadows.

Using the average sediment and mud content values quantified in this study, we can infer a total stock of $84–167\times10^{15}$ g DW of sediment and $10–21\times10^{15}$ g DW of mud under Mediterranean *P. oceanica* meadows (for a 475 cm sediment layer). Previous studies reported that the retention capacity of a *P. oceanica* meadow is up to 15 times higher than a barren bottom (Gacia et al., 1999), and sediments from unvegetated sites are coarser than those of seagrasses (De Falco et al., 2003). Given the importance of sediment resuspension processes in the Mediterranean littoral (Dauby et al., 1995; Gacia and Duarte, 2001), the retention capacity of *P. oceanica* meadows limits mud resuspension and its associated benefits, such as preventing the loss of beaches and the damage of adjacent communities, delaying dredging operations in harbors and marinas, and enhancing water transparency.

5. Conclusions

This study provides the first thorough description of a long continuous *P. oceanica* mat sequence. The coring method used proved to be efficient for sampling cores of up to 5 m long in shallow meadows (3–4 m depth), although it had some important limitations. Other coring techniques (e.g. vibrocoring) that allow a continuous long core to be sampled would substantially simplify post-sampling procedures.

The mat characteristics meet perfectly the requirements for a sediment to be considered a soil. Specifically, according to the requirements set by the World Reference Base for Soil Resources (FAO, Rome), the sediments under *P. oceanica* can be classified as a Limnic Subaquatic Histosols (Calcaric, Eutric).

The radiocarbon dating of this 475 cm core revealed a very consistent temporal sequence with an average resolution of ~8 y cm^{-1}. This study confirms that the *P. oceanica* mat fulfils the conditions for being an accurate and valuable palaeorecord that can be used to reconstruct oceanographic, climatic and ecological trends and patterns during the Late Holocene in the Mediterranean.

Although seagrass meadows cover a relatively small portion of the ocean (~ 1%; Green and Short, 2003), the results obtained in this study show that *P. oceanica* meadows play a significant role in the C cycle in Mediterranean coastal areas.

This study also gives further support to the already-recognized, key role seagrasses play in stabilizing the coast line and increasing water transparency by trapping and retaining large amounts of sediments over millennia.

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