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Location and Associated Carbon Storage of Erosional Escarpments of Seagrass *Posidonia* Mats

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Seagrasses of the genus *Posidonia* can form an irregular seascape due to erosional processes exposing thick walls of organic matter-rich soils. However, little is known about the location and characteristics of these particular formations. Here we provide comprehensive estimates of organic carbon (C_{org}) storage in *Posidonia oceanica* and *Posidonia australis* meadows, while providing insight into their location and mechanisms of formation, and highlighting future research directions. Erosional reef escarpments are restricted to shallow highly productive *P. oceanica* meadows from the Mediterranean Sea and *P. australis* meadows from the Indian Ocean, and sustain the existence of C_{org}-rich deposits in surrounding meadows. The thickness of the mat escarpments can reach up to 3 m and their length can vary from few to hundreds of meters. Mechanisms of formation appear to differ among sites, from naturally-induced escarpments by wave action and/or tidal flow to human-induced escarpments by dredging activities. The inter-twined remains of seagrass shoots within the sediment matrix consolidate the sandy substrate and hold the exposed *Posidonia* mat escarpments together, maintaining a semi-rigid structure. This phenomenon is unusual but of exceptional importance in marine biogeochemical cycles, revealing the largest C_{org} sinks among seagrasses worldwide (ranging from 15 to 176 kg C_{org} m^{-2} in 2 m-thick mats accumulated at 2–249 g C_{org} m^{-2} yr^{-1} over 300–3000 yr).

Keywords: ecosystem services, biogeochemical cycles, blue carbon, *Posidonia oceanica*, *Posidonia australis*, Mediterranean Sea, Indian Ocean

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INTRODUCTION

Seagrasses form dense and extensive coastal meadows extending from intertidal areas down to 40 m depth worldwide except in the Antarctica (Green and Short, 2003). The meadows are ecologically important as they support coastal communities essential for maintaining high biodiversity levels (Hemminga and Duarte, 2000). Seagrasses also provide other key ecosystem services such as shoreline protection against erosion by substrate stabilization and hydrodynamic energy dissipation (Green and Short, 2003; Boudouresque et al., 2014), and by providing a source of carbonate sand for beach formation (Canals and Ballesteros, 1997; Tigny et al., 2007).

Additionally, and noteworthy, seagrasses capacity to sequester and store organic carbon (C_{org}) contributes to the mitigation of anthropogenic CO_2 emissions (Fourqurean et al., 2012; Duarte et al., 2013). In this sense, the leaf sheaths, rhizomes and roots detritus of the Mediterranean endemic *Posidonia oceanica* form a highly organic structure known as mat (Pérès and Picard, 1964; Boudouresque and Meinesz, 1982). The organic-rich deposits beneath the *P. oceanica* canopy can reach up to 13 m-thick and 6000 years of age, and contain massive carbon storage ranging from 40 to 770 kg C_{org} m^{-2} (Mateo et al., 1997; Lo Iacono et al., 2008; Serrano et al., 2014); little is known about the C_{org} storage and thickness of *Posidonia australis* mats (Paling and McComb, 2000). The mats of *P. oceanica* have started to be studied from palaeoecological viewpoints only recently (Lo Iacono et al., 2008; López-Sáez et al., 2009; Serrano et al., 2012, 2013; López-Merino et al., 2015), while the study of *P. australis* mats is at its onset (Rozaimi et al., 2013; Marbà et al., 2015; Serrano et al., 2016).

Several factors are involved in the accumulation of organic-rich material in the *P. oceanica* mat, resulting from the millenarian balance between material accretion (detritus and sediment), decomposition and erosion (Duarte and Cebrian, 1996; Mateo et al., 1997, 2006; Pergent et al., 1997; Gacia et al., 2002; Boudouresque et al., 2006). On the one hand, the rhizomes can reach lengths over 1 m, with both plagiotropic (horizontal) and orthotropic (vertical) growth (Pergent and Pergent-Martini, 1990), forming an extensive plant detritus network embedded within an inorganic sediment matrix (Pérès and Picard, 1964). On the other hand, plant detritus show a reduced decay inside the mat (Serrano et al., 2012) due to the refractory nature of the plant tissue (Kuo, 1978; Kuo and Cambridge, 1978; Harrison, 1989; Klap et al., 2000) and the anoxic environment inside the mat (Mateo et al., 1997, 2006). Although other seagrasses accumulate C_{org} (Lavery et al., 2013), no records for the storage of massive C_{org} have been reported so far for any other seagrass species but *P. oceanica* (Fourqurean et al., 2012). However, large quantities of decay-resistant organic matter have been reported for *P. australis* and *Thalassodendron ciliatum* (Mateo et al., 2006).

Seagrass meadows typically form a relatively homogeneous but highly diverse habitat in the near-shore environment, with the upper and lower depth limits determined, generally, by hydrodynamic conditions and light limitation (Duarte, 1991; Collier et al., 2008). Under some circumstances, the erosion of seagrass meadows can expose the mats creating erosional escarpments (Pérès and Picard, 1964; Mateo et al., 1997). The existence of exposed mat walls in *P. oceanica* meadows in the Mediterranean Sea and their erosive mechanism of formation were first described by Pérès and Picard (1964). However, the existence of escarpments of remarkable dimensions (up to 3 min height), and their process of formation and evolution remains largely unknown (Boudouresque et al., 2014). In this study, we want to start filling this gap by providing new information on *P. australis* (Indian Ocean) and *P. oceanica* (Mediterranean Sea) mat escarpments. Aiming to identify and compare the reef structures they form, we have collected literature data and complemented it with the study of new mats in order to unravel potential mechanisms of formation and carbon storage capacity, providing our viewpoints based on existing knowledge, field observations and expert judgment, discussing current advances and future research directions.

MATERIALS AND METHODS

P. australis mats were sampled at Oyster Harbor, Big Lagoon, Waychinicup Inlet, and Port Pirie in Australia (Image 1 and Data Sheet 1). The Big Lagoon (Shark Bay) is a sheltered marine embayment consisting in a deep central channel surrounded by shallow seagrass meadows, while the Oyster Harbor and Waychinicup Inlet are estuaries, and the Port Pirie is a large marine embayment. The coring of the mats was carried out at a water depth of 2–3 m on continuous meadows, within 10 m of mat escarpments (vertical coring).

Up to 3 m-long mat cores were collected by manual percussion and rotation using 65 mm-diameter PVC pipes. Compression of sediments during coring was corrected by distributing the spatial discordances proportionally between the expected and the observed sediment layers (Glew et al., 2001). The overall degree of core shortening was <30%. All results reported refer to the decompressed depths.

P. oceanica mats were sampled at Mellieha Bay and Salina Bay in Malta (Mediterranean Sea; Image 1 and Data Sheet 1). The sites consist of relatively sheltered sub-tidal basins. The mat cores were taken horizontally from exposed vertical mat walls (2–3 m water depth on top of the mat wall), using hand-operated PVC corers (100 cm long; 80 mm diameter). Three horizontal cores were sampled down the mat escarpment at 16, 73, and 145 cm depth at Salina Bay, and at 10, 40, 80, 120, 160, 200, and 230 cm depth at Mellieha Bay.

Cores were sealed and stored at 5°C before processing. The *P. australis* cores (vertical coring) were sub-sampled at 1 cm intervals. The outermost 10 cm of the horizontal *P. oceanica* cores were discarded to eliminate possible contamination with recent material; the remainder material from each level was homogenized and sub-sampled for analysis.

Samples were weighed before and after oven drying to constant weight at 70°C, and ground in a ball mill grinder. For organic carbon (C_{org}) analysis, 1 g of ground sample was acidified with 4% HCl, centrifuged (5 min at 3400 rpm), and the supernatant removed by pipette. The sample was then washed with Milli-Q water, centrifuged, and the supernatant removed again. The residual samples were re-dried and encapsulated for C_{org} analysis using a Micro Cube elemental analyzer (Elementar Analysensysteme GmbH) at the UC Davis Facilities. The content of C_{org} (in %) was calculated for the bulk (pre-acidified) sediment.

Fourteen samples of *Posidonia* sheath macro-remains, and eight samples of shells were radiocarbon dated following standard procedures (Stuiver and Pollack, 1977, Data Sheet 2). The sheath fibers and shells were rinsed in Milli-Q water, sonicated for 5 min to remove inorganic particles, and inspected for attached contaminants. The samples were dried at 60°C before radiocarbon dating. The dates were calibrated using CALIB 7.1 software with the MARINE13.14C curve (Stuiver and Reimer, 1993; Reimer et al., 2013) and corrected for the local

DeltaR by subtracting 30–91 years at Australia (Bowman, 1985; Squire et al., 2013) and 70 years at Malta (Siani et al., 2000). Dates are expressed as calibrated years BP. The calibrated ages were used to produce age–depth models (linear regression).

Because the thickness of sampled mat varied among sites, we normalized the substrate thickness over which the C_{org} stocks and accumulation rates were calculated to allow comparisons. The C_{org} inventories per unit area (kg m^{-2}) were estimated by multiplying the sediment dry bulk density (g cm^{-3}) by the C_{org} concentration, and then normalized to g C_{org} m^{-2} (i.e., cumulative mass in a soil thickness of 2 m). The long-term accumulation rates (g m^{-2} yr^{-1}) of C_{org} were calculated by multiplying the average C_{org} concentration by the sediment accumulation rates. Previously reported C_{org} stocks and accumulation rates in other *P. oceanica* mat sediment cores were also standardized to 2 m-thick deposits and compiled in **Table 1**. ANOVA was applied to test for any significant effect of species composition (*P. oceanica* and *P. australis*) on average C_{org} stocks and accumulation rates.

Lifetime observations of mat escarpments in *Posidonia* meadows made by the authors of this manuscript are described. The maximum height of the reef escarpments surveyed was measured *in situ* and the length was estimated from combining *in situ* observations and aerial imagery.

RESULTS AND DISCUSSION

Exposed reef escarpments are found in both *P. australis* and *P. oceanica* meadows (**Figure 1**). However, reef escarpments are not always present in seagrass and are restricted to highly productive *Posidonia* meadows that have likely been located in shallow (i.e., <5 m depth) and relatively protected areas for the last 1000–4000 years (Data Sheet 2), which supported seagrass productivity and stability. The formation of these erosional structures appears to be related to hydrodynamic energy over present or centennial time scales (as either continuous or pulse events; Pérès and Picard (1964) or dredging activities, which can erode the edge of the meadow exposing the organic-rich deposits. The exposed face of seagrass mat is held together by the inter-twined remains of seagrass tissues, avoiding collapse and maintaining a semi-rigid structure, which is susceptible to erosion (i.e., in consolidated sediments) and can lead to the formation of vertical escarpments ranging from 1 to 3 m in thickness, and from <100 m in length in *P. oceanica* to >500 m in *P. australis* meadows. Reports on escarpment of this size are not common and have only previously been described in the Mediterranean Sea, in particular in France (Molinier and Picard, 1952; Picard, 1953; Boudouresque et al., 1980, 1985, 1990; Boudouresque and Meinesz, 1982; Belsher et al., 2005), Spain (Mateo et al., 1997; Ribera et al., 1997; Serrano et al., 2014), and Italy (Mateo et al., 1997). Based on our observations we describe the existence of *P. oceanica* mat escarpments in several additional locations around the Mediterranean Sea. Additionally, we have described for the first time escarpments in *P. australis* in Australia: Big Lagoon, Waychinicup Inlet, Cheynes Bay, and Port Broughton (Image 1 and Data Sheet 1). Although, the dataset compiled provides a comprehensive summary, further studies are required to identify and describe erosional escarpments in seagrass meadows.

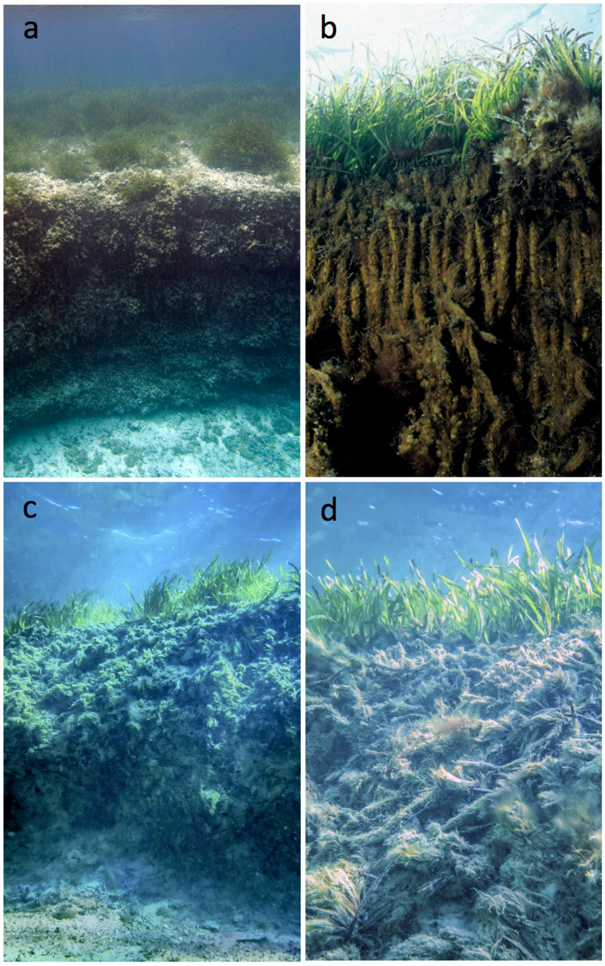

FIGURE 1 | Erosional escarpment in a *P. oceanica* meadow in Es Pujols Cove (Formentera, Balearic Islands, Spain) illustrating the organic-rich soils (A,B), Erosional escarpment in a *P. australis* meadow in Big Lagoon (Shark Bay, Western Australia; C,D). The water depth at the top of the formation is 3 m, the exposed face of the mat has a thickness of 2.7 m and the age of the base of the exposure is 1200 cal. yr BP. The water depth at the top of the formation is 2 m, the exposed face has a thickness of 2.5 m and the age at the base of the exposure is 4000 cal. yr BP. Note the vertical rhizomal growth of *P. oceanica* **(B)** compared to the horizontal rhizomal growth of *P. australis* **(D)**. Photo credit: M. A. Mateo **(A)**, *E. Ballesteros* **(B)**, *P. Lavery* **(C)**, and *O. Serrano* **(D)**.

The mechanisms of formation of erosional escarpments appear to differ among sites. In *P. australis* meadows at Big Lagoon (Shark Bay), tidal currents (tides up to 2 m) have created a deep channel allowing water exchange between the lagoon and the ocean. The channel passes through the shallow bank of seagrass, with water flow eroding and exposing the seagrass mats. At Cheynes Bay and Waychinicup Inlet (Albany), current and wave action could also lead to the erosion of *P. australis* meadows and the formation of reef escarpments up to 3 m-thick. However, severe river discharges could also explain the formation of mat

TABLE 1 | Compilation of organic carbon (C_{org}) stocks and accumulation rates in *P. oceanica* and *P. australis* meadows.

Species	Location	Water depth (m)	Mat thickness studied (cm)	Mat acc. rates (mm yr^{-1})	C_{org} acc. rates (g m^{-2} yr^{-1})	C_{org} inventory (kg m^{-2})
P. oceanica	[a]Cala Culip (Spain)[1]	4	160	0.6	9	30
	*[b]Campello (Spain)[1]	3	200	2.0	115	115
	*[b]Tabarca Is. North (Spain)[1]	5	170	1.1	62	113
	*[b]Tabarca Is. South (Spain)[1]	1.5	100	1.9	105	110
	[a]Medas Is. (Spain)[1]	14	200	0.8	13	33
	*[b]Portlligat (Spain)[1]	3	135	4.1	76	37
	*[b]Villajoyosa (Spain)[2]	7	190	1.9	40	42
	*[a]Portlligat (Spain)[3]	3	496	1.1	18	33
	*[a]Portlligat (Spain)[4]	3	475	1.3	22	33
	*[b]Talamanca Cove (Spain)[5]	2	270	2.3	202	176
	*[b]Es Pujols Cove (Spain)[5]	2	270	1.7	103	121
	*[b]Ischia (Italy)[1]	10	320	1.7	30	35
	*[b]Mellieha Bay (Malta)[6]	10	230	4.9	249	102
	*[b]Salina Bay (Malta)[6]	2	154	4.0	133	67
	Average ± *SE*	5	247 ± 36	2.1 ± 0.4	84 ± 20	75 ± 13
P. australis	[a]Oyster Harbor (Australia)[6]	2	150	0.49	4	15
	*[a]Waychinicup Inlet (Australia)[6]	2	210	0.43	5	24
	[a]Port Pirie (Australia)[6]	3	110	0.13	2	27
	*[a]Port Broughton	2	200	2.5	40	32
	*[a]Big Lagoon (Australia)[6]	2	280	0.51	7	29
	Average ± *SE*	2.2	190 ± 29	0.8 ± 0.4	12 ± 7	25 ± 3

The C_{org} inventories and C_{org} accumulation rates are normalized to 2 m-thick mat deposits.

** Study sites with exposed reef-barrier formations.*

[a] *Vertical coring in the top of the meadow.*

[b] *Horizontal coring in the mat escarpment.*

[1] *Mateo et al., 1997;* [2] *Mateo et al., 2005;* [3] *Lo Iacono et al., 2008;* [4] *Serrano et al., 2012;* [5] *Serrano et al., 2014;* [6] *This study.*

escarpments at Waychinicup Inlet. In *P. oceanica* meadows of the Mediterranean Sea, where tides are <0.5 m, escarpment formation is most likely related to waves and associated currents, in particular during extreme storm events. Human activities (e.g., dredging) that erode the base of the meadow, can also led to the formation of mat escarpments. At Port Broughton (Adelaide), and Sanitja Cove (Balearic Islands) dredging to clear shipping channel and boating activities led to the formation of mat escarpments.

Although, the mechanisms of formation of the *Posidonia* escarpments could differ among places, their dynamics could share some similarities (i.e., collapses due to erosion of its base by hydrodynamic action) with the formation of cliffs in rocky shores (Stephenson, 2000) or wrack banquettes along the beaches (Mateo et al., 2003). It seems probable that the hydrodynamic energy gradually erodes the base of the escarpment until the top edge of the mat collapses and, consequently, the meadow retreats (Pérès and Picard, 1964; Boudouresque et al., 1980). The curve shapes present along the base of the escarpments and the occasional presence of loose fragments of mat with living seagrass at the base of the escarpments supports this hypothesis. Further research aiming to unravel the mechanisms of formation, dynamics and processes within mat escarpments is required to test the hypotheses described above.

According to the age-depth models, accumulation rates in *Posidonia* meadows (i.e., mats close to the upper limit of seagrass distribution) ranged from 0.13 to 4.9 mm yr^{-1} (**Table 1**). The *P. australis* meadows sampled in this study contained in average 25 ± 3 kg C_{org} m^{-2} (in 2 m-thick deposits) accumulated at a rate of 12 ± 7 g C_{org} m^{-2} yr^{-1} over 1000–3500 years, the largest stocks recorded in seagrasses other than *P. oceanica* meadows (averaged 75 ± 13 kg C_{org} m^{-2} and 84 ± 20 g C_{org} m^{-2} yr^{-1}; **Table 1**). The comparison of C_{org} storage capacity and accumulation rates by *P. australis* and *P. oceanica* meadows provide new insights into the significant differences in C_{org} storage potential among *Posidonia* seagrasses ($P < 0.001$ for both C_{org} storage and accumulation rates). The C_{org} storage in *P. oceanica* and *P. australis* meadows is exceptional compared to other seagrass species (ranging from 0.6 to 12 kg C_{org} m^{-2} in 1 m-thick deposits; Lavery et al., 2013; Campbell et al., 2015; Miyajima et al., 2015), and the presence of an exposed mat escarpment provides an early indication of rich C_{org} deposits beneath the surrounding meadows. Although, in this study we only surveyed directly mat escarpments (i.e., by horizontal coring) in Malta and Balearic Islands, we assumed that the C_{org} contents measured in the mats near the escarpments (i.e., by vertical coring) are representative of the C_{org} content in meadows close to the upper limit of seagrass distribution where escarpments can be found. The erosive nature of escarpments implies that their edges have retracted over time, and the exposure of the escarpments to oxic conditions and irradiance may lead to a shift in the C_{org} composition and accumulation in these areas due to the growth of e.g. algae and microbes compared to intact C_{org} stores underneath the meadows, but scientific evidence is lacking to support this hypothesis.

The three-fold higher C_{org} stores in *P. oceanica* compared to *P. australis* could be attributed to the higher sediment accumulation rates in *P. oceanica* meadows (2.1 ± 0.4 mm yr^{-1}), enhanced by their vertical rhizomal growth (i.e., orthotropic) compared to the horizontal rhizomal growth (i.e., plagiotropic) in *P. australis* meadows (0.8 ± 0.4 mm yr^{-1}; **Table 1**; Gobert et al., 2006). In **Figure 1**, we highlight the differences in the rhizomal growth between the two *Posidonia* species. The higher mat accumulation rate of *P. oceanica* meadows could also contribute to a greater preservation of C_{org} stores after burial, as a result of more rapid burial of C_{org} into anoxic conditions (i.e., typically occurring at about 5 cm depth in the mat; Mateo et al., 2006). In addition, the higher belowground biomass of *P. oceanica* (1610 g m^{-2}; Duarte and Chiscano, 1999) compared to *P. australis* (658 g m^{-2}; Paling and McComb, 2000) may contribute to the higher C_{org} stores in the Mediterranean species. The geomorphological setting (e.g., run-off, hydrodynamic energy and water depth) in which seagrass meadows are found can influence the C_{org} storage capacity of seagrasses (Serrano et al., 2015). Although, the number of cores and species studied in coastal and estuarine ecosystems was unbalanced (i.e., *P. oceanica* dominate in coastal habitats and *P. australis* dominate in estuarine habitats) and therefore we were not able to test the effects of coastal geomorphology on C_{org} storage, further studies are required to address its implications. According to the curve of the Holocene sea level change inferred along the Mediterranean (Lambeck and Bard, 2000) and Australian (Lambeck and Nakada, 1990) coasts, the sea level was constant since 6000–4000 years ago. Thus, assuming that seagrasses have been present at the same locations since the Mid-Holocene, the maximum potential thickness of seagrass mats is estimated to be 8 to 13 m for *P. oceanica* and 3 to 5 m for *P. australis*, based on the mat accumulation rates compiled in our study. At these mat depths, the potential carbon stocks would be 315–473 kg C_{org} m^{-2} in *P. oceanica* and 40–60 kg C_{org} m^{-2} in *P. australis*. Previous studies reported 691–770 kg C_{org} m^{-2} in 8–13 m thick deposits in *P. oceanica* based on the exceptional meadows at Balearic Island (Serrano et al., 2014), and from Rozaimi et al. (2016) it is possible to estimate 22–36 kg C_{org} m^{-2} in 3–5 m thick deposits in *P. australis*. However, the ranges reported in our study encompass several meadows around the Mediterranean Sea and Australia and therefore constitute more comprehensive estimates of the C_{org} storage potential of *P. oceanica* and *P. australis*.

In summary, we conclude that exposed mat escarpments up to 3 m in height in seagrass *Posidonia* are unusual but of exceptional importance in marine biogeochemical cycles, preluding the largest carbon sinks among seagrasses worldwide. Further surveys are required to identify additional seagrass escarpments along the coasts, and to gain new insights into their ecology and mechanisms of formation.

AUTHOR CONTRIBUTIONS

Conceived and designed the experiments: OS, PL, and MM; Performed the experiments: OS, PL, LL-M, EB, and MM. Analyzed the data: OS. All authors contributed reagents, materials and analysis tools and wrote the paper.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2016.00042

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