Location and associated carbon storage of erosional escarpments of seagrass Posidonia mats

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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*<sub>org</sub>) 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*<sub>org</sub>-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*<sub>org</sub> sinks among seagrasses worldwide (ranging from 15 to 176 kg *C*<sub>org</sub> m<sup>−2</sup> in 2 m-thick mats accumulated at 2–249 g *C*<sub>org</sub> m<sup>−2</sup> yr<sup>−1</sup> over 300–3000 yr).

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

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 \( (C_{\text{org}}) \) contributes to the mitigation of anthropogenic \( \text{CO}_2 \) emissions (Fourqurean et al., 2012; Duarte et al., 2013). In this sense, the leaf sheaths, rhizomes and roots detritus of the Mediterranean endemic \textit{Posidonia oceanica} form a highly organic structure known as mat (Pérès and Picard, 1964; Boudouresque and Meinesz, 1982). The organic-rich deposits beneath the \textit{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 \( C_{\text{org}} \) m\(^{-2} \) \cite{Mateo1997, Serrano2014}; little is known about the \( C_{\text{org}} \) storage and thickness of \textit{Posidonia australis} mats \cite{Paling2000}. The mats of \textit{P. oceanica} have started to be studied from palaeoecological viewpoints only recently \cite{LoIacono2008, López-Sáez2009, Serrano2012, Serrano2013, López-Merino2015}, while the study of \textit{P. australis} mats is at its onset \cite{Rozaimi2015, Marba2015, Serrano2016}.

Several factors are involved in the accumulation of organic-rich material in the \textit{P. oceanica} mat, resulting from the millenarian balance between material accretion (detritus and sediment), decomposition and erosion \cite{Duarte1991, Duarte1996, Mateo1997, Pergent1997, García2002, Boudouresque2006}. On the one hand, the rhizomes can reach lengths over 1 m, with both plagiotropic (horizontal) and orthotropic (vertical) growth \cite{Pergent1990}, forming an extensive plant detritus network embedded within an inorganic sediment matrix \cite{Pérès1964}. On the other hand, plant detritus show a reduced decay inside the mat \cite{Serrano2012} due to the refractory nature of the plant tissue \cite{Kuo1978, Kuo1978a, Harrison1989, Klap2000} and the anoxic environment inside the mat \cite{Mateo1997, Mateo2006}. Although other seagrasses accumulate \( C_{\text{org}} \) \cite{Laverty2013}, no records for the storage of massive \( C_{\text{org}} \) have been reported so far for any other seagrass species but \textit{P. oceanica} \cite{Fourqurean2012}. However, large quantities of decay-resistant organic matter have been reported for \textit{P. australis} and \textit{Thalassodendron ciliatum} \cite{Mateo2006}.

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 \cite{Duarte1991, Collier2008}. Under some circumstances, the erosion of seagrass meadows can expose the mats creating erosional escarpments \cite{Pérès1964, Mateo1997}. The existence of exposed mat walls in \textit{P. oceanica} meadows in the Mediterranean Sea and their erosive mechanism of formation were first described by Pérès and Picard \cite{Pérès1964}. However, the existence of escarpments of remarkable dimensions \( \text{up to 3 m} \) height, and their process of formation and evolution remains largely unknown \cite{Boudouresque2014}. In this study, we want to start filling this gap by providing new information on \textit{P. australis} (Indian Ocean) and \textit{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

\textit{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 \cite{Glew2001}. The overall degree of core shortening was <30%. All results reported refer to the decompressed depths.

\textit{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 \( \text{(2–3 m water depth on top of the mat wall)} \), using hand-operated PVC corers \( \text{(100 cm long; 80 mm diameter)} \). 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 \textit{P. australis} cores (vertical coring) were sub-sampled at 1 cm intervals. The outermost 10 cm of the horizontal \textit{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 \( (C_{\text{org}}) \) analysis, 1 g of ground sample was acidified with 4% HCl, centrifuged \( \text{(5 min at 3400 rpm)} \), 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 \( C_{\text{org}} \) analysis using a Micro Cube elemental analyzer \cite{Elementar} at the UC Davis Facilities. The content of \( C_{\text{org}} \) \( \text{(in %)} \) was calculated for the bulk \( \text{(pre-acidified)} \) sediment.

Fourteen samples of \textit{Posidonia} sheath macro-remains, and eight samples of shells were radiocarbon dated following standard procedures \cite{Stuiver1977, DataSheet2}. 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 \cite{Stuiver1993, Reimer2013} 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 \( C_{\text{org}} \) stocks and accumulation rates were calculated to allow comparisons. The \( C_{\text{org}} \) inventories per unit area (kg m\(^{-2}\)) were estimated by multiplying the sediment dry bulk density (g cm\(^{-3}\)) by the \( C_{\text{org}} \) concentration, and then normalized to g \( C_{\text{org}} \) m\(^{-2}\) (i.e., cumulative mass in a soil thickness of 2 m). The long-term accumulation rates (g m\(^{-2}\) yr\(^{-1}\)) of \( C_{\text{org}} \) were calculated by multiplying the average \( C_{\text{org}} \) concentration by the sediment accumulation rates. Previously reported \( C_{\text{org}} \) stocks and accumulation rates in other \( P. \text{oceanica} \) 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 (\( P. \text{oceanica} \) and \( P. \text{australis} \)) on average \( C_{\text{org}} \) stocks and accumulation rates.

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

### RESULTS AND DISCUSSION

Exposed reef escarpments are found in both \( P. \text{australis} \) and \( P. \text{oceanica} \) meadows (Figure 1). However, reef escarpments are not always present in seagrass and are restricted to highly productive \textit{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 \( P. \text{oceanica} \) to >500 m in \( P. \text{australis} \) 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 \( P. \text{oceanica} \) mat escarpments in several additional locations around the Mediterranean Sea. Additionally, we have described for the first time escarpments in \( P. \text{australis} \) 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.

The mechanisms of formation of erosional escarpments appear to differ among sites. In \( P. \text{australis} \) 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 \( P. \text{australis} \) meadows and the formation of reef escarpments up to 3 m-thick. However, severe river discharges could also explain the formation of mat
escarpments at Waychincup Inlet. In \textit{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
lead 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 \textit{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
\textit{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
\textit{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 \textit{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 \textit{P. australis} and \textit{P. oceanica} meadows provide new insights
into the significant differences in C$_{org}$ storage potential among
\textit{Posidonia} seagrasses (P < 0.001 for both C$_{org}$ storage and
accumulation rates). The C$_{org}$ storage in \textit{P. oceanica} and \textit{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

**TABLE 1** | Compilation of organic carbon (C$_{org}$) stocks and accumulation rates in \textit{P. oceanica} and \textit{P. australis} meadows.

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Water depth (m)</th>
<th>Mat thickness studied (cm)</th>
<th>Mat acc. rates (mm yr$^{-1}$)</th>
<th>C$_{org}$ acc. rates (g m$^{-2}$ yr$^{-1}$)</th>
<th>C$_{org}$ inventory (kg m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>\textit{P. oceanica}</td>
<td>aCa Chalupa (Spain)$^1$</td>
<td>4</td>
<td>160</td>
<td>0.6</td>
<td>9</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>bCampello (Spain)$^1$</td>
<td>3</td>
<td>200</td>
<td>2.0</td>
<td>115</td>
<td>115</td>
</tr>
<tr>
<td></td>
<td>cTabarca Is. North (Spain)$^1$</td>
<td>5</td>
<td>170</td>
<td>1.1</td>
<td>62</td>
<td>113</td>
</tr>
<tr>
<td></td>
<td>dTabarca Is. South (Spain)$^1$</td>
<td>1.5</td>
<td>100</td>
<td>1.9</td>
<td>105</td>
<td>110</td>
</tr>
<tr>
<td></td>
<td>eMedas Is. (Spain)$^1$</td>
<td>14</td>
<td>200</td>
<td>0.8</td>
<td>13</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>fPortlligat (Spain)$^1$</td>
<td>3</td>
<td>135</td>
<td>4.1</td>
<td>76</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>gVillajoyosa (Spain)$^2$</td>
<td>7</td>
<td>190</td>
<td>1.9</td>
<td>40</td>
<td>42</td>
</tr>
<tr>
<td></td>
<td>hPortlligat (Spain)$^3$</td>
<td>3</td>
<td>496</td>
<td>1.1</td>
<td>18</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>iPortlligat (Spain)$^4$</td>
<td>3</td>
<td>475</td>
<td>1.3</td>
<td>22</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>jTalamanca Cove (Spain)$^5$</td>
<td>2</td>
<td>270</td>
<td>2.3</td>
<td>202</td>
<td>176</td>
</tr>
<tr>
<td></td>
<td>kEs Pujols Cove (Spain)$^6$</td>
<td>2</td>
<td>270</td>
<td>1.7</td>
<td>103</td>
<td>121</td>
</tr>
<tr>
<td></td>
<td>lPischia (Italy)$^5$</td>
<td>10</td>
<td>320</td>
<td>1.7</td>
<td>30</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>mMellieha Bay (Malta)$^6$</td>
<td>10</td>
<td>230</td>
<td>4.9</td>
<td>249</td>
<td>102</td>
</tr>
<tr>
<td></td>
<td>nSalina Bay (Malta)$^6$</td>
<td>2</td>
<td>154</td>
<td>4.0</td>
<td>133</td>
<td>67</td>
</tr>
<tr>
<td></td>
<td>Average ± SE</td>
<td>5</td>
<td>247 ± 36</td>
<td>2.1 ± 0.4</td>
<td>84 ± 20</td>
<td>75 ± 13</td>
</tr>
<tr>
<td>\textit{P. australis}</td>
<td>aOyster Harbor (Australia)$^6$</td>
<td>2</td>
<td>150</td>
<td>0.49</td>
<td>4</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>bWaychincup Inlet (Australia)$^6$</td>
<td>2</td>
<td>210</td>
<td>0.43</td>
<td>5</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>cPort Pirie (Australia)$^6$</td>
<td>3</td>
<td>110</td>
<td>0.13</td>
<td>2</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>dPort Broughton</td>
<td>2</td>
<td>200</td>
<td>2.5</td>
<td>40</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>eBig Lagoon (Australia)$^6$</td>
<td>2</td>
<td>280</td>
<td>0.51</td>
<td>7</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>Average ± SE</td>
<td>2.2</td>
<td>190 ± 29</td>
<td>0.8 ± 0.4</td>
<td>12 ± 7</td>
<td>25 ± 3</td>
</tr>
</tbody>
</table>

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

$^1$ Vertical coring in the top of the meadow.

$^2$ Horizontal coring in the mat escarpment.

$^3$ Mateo et al., 1997; $^4$ Mateo et al., 2005; $^5$ Lo Iacono et al., 2008; $^6$ Serrano et al., 2012; $^7$ Serrano et al., 2014; $^8$ This study.
time, and the exposure of the escarpments to oxic conditions and irradiance may lead to a shift in the $C_{\text{org}}$ composition and accumulation in these areas due to the growth of e.g. algae and microbes compared to intact $C_{\text{org}}$ stores underneath the meadows, but scientific evidence is lacking to support this hypothesis.

The three-fold higher $C_{\text{org}}$ stores in *P. oceanica* compared to *P. australis* could be attributed to the higher sediment accumulation rates in *P. oceanica* meadows ($2.1 \pm 0.4$ 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 ($0.8 \pm 0.4$ 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 $C_{\text{org}}$ stores after burial, as a result of more rapid burial of $C_{\text{org}}$ into anoxic conditions (i.e., typically occurring at about 5 cm depth in the mat; Mateo et al., 2006). In addition, the higher subequatorial 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 $C_{\text{org}}$ 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 $C_{\text{org}}$ 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 $C_{\text{org}}$ 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 $C_{\text{org}}$ m$^{-2}$ in *P. oceanica* and $40-60$ kg $C_{\text{org}}$ m$^{-2}$ in *P. australis*. Previous studies reported 691–770 kg $C_{\text{org}}$ 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 $C_{\text{org}}$ 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 $C_{\text{org}}$ 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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