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Effect of environmental factors (wave exposure and depth) and anthropogenic pressure in the C sink capacity of *Posidonia oceanica* meadows

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Abstract

Seagrass are among the most important natural carbon sinks on Earth with *Posidonia oceanica* (Mediterranean Sea) considered as the most relevant species. Yet, the number of direct measurements of organic carbon burial rates in *P. oceanica* is still scarce and the effect of local environmental factors remains largely unexplored. In addition, *P. oceanica* meadows are declining due to the increase in anthropogenic pressure in coastal areas during the last century. The aim of this study is to assess the recent carbon sink capacity of *P. oceanica* and particularly the effect of human pressure and two environmental factors, water depth and exposure to wave energy (based on a fetch index), on the carbon burial rate since 1900. We conducted an extensive survey of sediment cores in meadows distributed across a gradient of depth, fetch, and human pressure around The Balearic Islands. Sediment and carbon accumulation rates were obtained from ^{210}Pb concentrations profiles. Top-30 centimeters carbon stocks (6.1 ± 1.4 kg C m^{-2}) and burial rates (26 ± 6 g C m^{-2} yr^1) varied up to fivefold across meadows. No significant effect of water depth in carbon burial rates was observed. Although fetch was significantly correlated with sediment mean grain size, confirming the effect of wave exposure in the patterns of sedimentation, fetch alone could not explain the differences in carbon burial rates among the meadows examined. Human pressure affected carbon burial rates, leading to increased rates since the onset of the rise in anthropogenic pressure, particularly so in sheltered meadows supporting high human pressure.

Seagrass meadows rank among the most intense natural carbon sinks of the biosphere (Nellemann et al. 2009; Fourqurean et al. 2012; Duarte et al. 2013a). Due to their high carbon sink capacity and their broad distribution along the coastal areas of all continents, except the Antarctica (Hemminga and Duarte 2000), seagrass meadows contribute about 50–64% of the organic carbon (C$_{org}$) sequestered annually by coastal vegetated ecosystems (Duarte et al. 2013b) and bury 20% of the carbon buried in the global ocean (Duarte et al. 2005; Kennedy et al. 2010).

The endemic Mediterranean seagrass, *Posidonia oceanica*, stands out as the species supporting the highest carbon burial rates (Duarte et al. 2005; Lavery et al. 2013) and the largest sediment organic carbon stocks (Fourqurean et al. 2012; Lavery et al. 2013) among all seagrass studied thus far.

P. oceanica develops millenary clones (Arnaud-Haond et al. 2012), with shoots up to tens of decades in age (Marbà et al. 2005) connected by thick and robust rhizomes that extend both horizontally and vertically, forming reefs that can reach 6 m thick (Lo Iacono et al. 2008). The massive carbon stocks accumulated by *P. oceanica* have been explained on the basis of intrinsic properties of the species, including its long life span, high productivity, high

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belowground biomass and recalcitrant nature of its tissues (Mateo et al. 2006) along with dense canopies that buffer particle resuspension (Gambi et al. 1990; Gacia et al. 1999; Terrados and Duarte 2000) while promoting particle trapping (Hendriks et al. 2008; Kennedy et al. 2010), high sedimentation rates and hence, high burial capacity (Mateo et al. 2006). However, estimates of C_{org} burial rates in *P. oceanica* meadows are still scarce (Mateo et al. 1997; Serrano et al. 2012) and the high variability in C_{org} burial rates identified across meadows (Mateo et al. 1997) suggests that the C_{org} sink capacity is also controlled by environmental factors, which are, as for other species, poorly understood (Macreadie et al. 2014).

A large number of environmental factors are likely to affect the carbon sink capacity of *P. oceanica* meadows. Among them, the exposure to waves, which determines the patterns of sedimentation and may lead to sediment resuspension and erosion during high-energy events (Van Keulen and Borowitzka 2003; Bradley and Houser 2009; Hansen and Reidenbach 2012). Indices of wave exposure, such as effective fetch, have been successfully used as predictors of sediment grain size and percentage of sediment organic carbon (% C_{org}) in seagrass meadows, where those with smaller sediment grain size and higher C_{org} concentration usually coincide with low-energy environments (Murphey and Fonseca 1995; Fonseca and Bell 1998). Because of this close coupling between sediment grain size and coastal hydrodynamics, grain size may be used as an indicator of hydrodynamic conditions (Cabaço et al. 2010). Hence, differences in wave exposure among locations may help explain differences in carbon burial rates among *P. oceanica* meadows. In addition, a recent study identified that water depth constrained the C sink capacity of seagrass meadows, observing higher stocks and burial rates in shallower meadows that tended to decrease toward deeper meadows (Serrano et al. 2014). This study attributed this finding to differences in light availability induced by the depth gradient (Serrano et al. 2014) as irradiance controls shoot density and net C balance (Alcoverro et al. 1995).

P. oceanica meadows are experiencing a widespread decline across the Mediterranean Sea, with over 1/3 of their cover lost over the past 50 yr (Marbà et al. 2014), consistent with global declining trends for seagrass meadows (Waycott et al. 2009). *P. oceanica* loss is largely attributable to anthropogenic pressures, such as eutrophication (Duarte 2002; Marbà et al. 2014), which in the Mediterranean Sea mainly derive from fast urbanization and intensive development of the tourism industry in coastal areas initiated around the 60s (Boudouresque et al. 2009).

The decline of *P. oceanica* meadows may imply the loss of its C_{org} sink capacity (Marbà et al. 2014) along with other ecosystem services. In addition, the increasing urbanization and usage of the coast may have affected the carbon burial capacity of *P. oceanica* meadows over time by altering the patterns of sedimentation and the inputs of autochthonous and allochthonous carbon into meadows sediments. High human activity usually enhances nutrient inputs to coastal areas (Bowen and Valiela 2001) that, when moderate, may favor seagrass productivity (Powell et al. 1989). On the contrary, an excess input of nutrients may lead to eutrophication, reducing water quality and seagrass production (Short and Burdick 1996) while increasing the load of allochthonous carbon such as phytoplankton and organic detritus (Borum 1985; Duarte et al. 1995) that may get trapped and buried in seagrass sediments.

The aim of this study is to assess the recent carbon sink capacity (stocks and burial rates) of *P. oceanica* meadows and particularly to assess the effect of human pressure and two environmental factors, water depth and exposure to wave energy (based on a fetch index), on the C_{org} burial rate since 1900. We do so by examining sediment cores across eleven *P. oceanica* meadows sampled along a gradient of water depth, wave exposure and level of human pressure in The Balearic Islands (Western Mediterranean) and by comparing the C_{org} burial between two periods: before and after human pressure increased at each site.

Methods

Description of study sites

The Balearic Islands rank among the top touristic destinations in Europe (Hof and Schmitt 2011). The tourism industry is the main economic sector in the region and has led to intensive urbanization during the last century (Pons et al. 2014), particularly in the coastal zone (Murray et al. 2008). Tourism in the Balearic Islands started booming around the 1960s (Rullan 1998), leading to a high influx of tourists during the summer period and an increase in population density in the coastal tourist areas, due to the arrival of rural islanders and migrants (Pons et al. 2014). As a result, in only 50 yr, the coastline has been rapidly transformed through intensive construction of tourist resorts and the development of urban areas (Pons et al. 2014). The Balearic Islands are also a globally significant spot for recreational boating (Balaguer et al. 2011), which delivers additional pressure to *P. oceanica* meadows through intensive anchoring (Ceccherelli et al. 2007; Montefalcone et al. 2008) and through the input of organic matter and nutrients through wastewater discharges (Matthew Leon and Warnken 2008) from boats and harbors.

Farmlands are mainly located inland (Basterretxea et al. 2010) and the influence of rivers and fresh water inputs in coastal water is minimal as the karstic condition of the sediment prevents the formation of perennial rivers (Kent et al. 2002) with only ephemeral streams forming in the wettest seasons (Basterretxea et al. 2010).
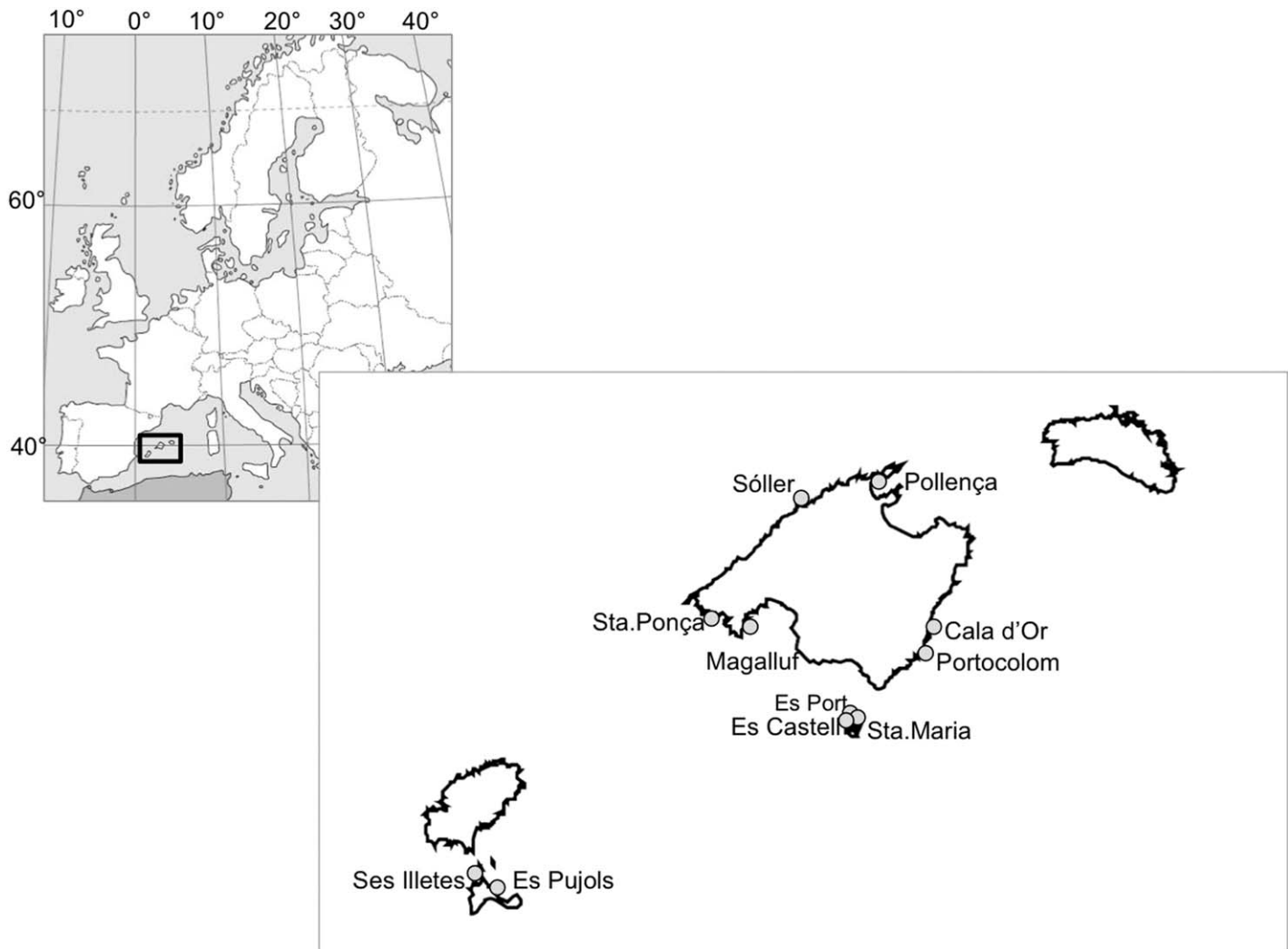
Fig. 1. Location of the sampling sites in the Balearic Islands.

Therefore, the degree of human influence in the coastal zone of the region of study is intimately related to tourism industry development and derived from a high population density, intensive urbanization and a high usage of coastal areas, including recreational boating. These factors are in fact among the most significant pressures to *P. oceanica* meadows identified in other regions of the Mediterranean Sea (Holon et al. 2015).

Eleven *P. oceanica* meadows were selected around the archipelago of The Balearic Islands, 6 in Mallorca, 2 in Formentera, and 3 in the Cabrera National Park (Fig. 1), distributed along a gradient of water depth, wave exposure and human pressure (Table 1).

Mallorca, is the largest island with 49% of the surface considered to be artificial or modified, built or transformed by human activities (Balaguer et al. 2008). Formentera is the less populated island from the Archipelago but supports intense pressure from summer tourism, including boat

effluence (e.g., Ses Illetes) and rapid urbanization of certain areas, such as Es Pujols (Morey et al. 1992; Roig-Munar et al. 2013).

The Archipelago of Cabrera is a non-permanently inhabited group of small islands used as an army station from 1940 until it was declared as a national park in 1991. Santa Maria bay, closed to visitors since 1993, and Es Castell, where anchoring is not permitted, represent the two most pristine *P. oceanica* meadows included in this study. The meadow at Es Port bay is, on the contrary, under a relatively higher level of human pressure as it is where the Park's visitor center and the main services are located and where visitors arriving by touristic ferries or sailing boats are allowed to moor in one of the 50 buoys available. Es Port waters receive the sewage produced by visitors in moored boats, few of which are equipped with holding tanks (Marbà et al. 2002) and the outflow of the treated sewage produced by the visitors on land (PNMTAC 2009).

Table 1. Location and main features of sampled seagrass meadows. Wave exposure (fetch), water column depth, human pressure (standardized) index, level of human pressure assigned to each meadows and the estimated year of increase of human pressure ($Year_{HP}$) are the main factors assessed. Meadow shoot population parameters (avg ± SE), density (shoot m^{-2}), net population growth (yr^{-1}) and surface area covered (%) are also provided. Data on shoot density and population growth are estimates from yearly surveys of permanent plots in each meadow during the last 3–11 yr before the study was conducted (Marbà et al. unpubl.) and data on % surface covered correspond to two field campaigns (years 2008 and 2009) and one field campaign in Es Port (Cabrera) in 2000 (Marbà et al. 2006, unpubl.).

		Meadow geophysical parameters			Human pressure			Meadow shoot population		
Station	Island	Latitude/longitude	Fetch (km)	Depth (m)	Index	Level	$Year_{HP}$	Density (shoots m^{-2})	Net population growth (yr^{-1})	% Surface covered
Pollença	Mallorca	39°54′16.97″N/3°05′34.51″E	16.63	4	9.8	Very high	1965	643 ± 75	−0.04 ± 0.06	92 ± 9
Sta.Ponça	Mallorca	39°30′48.37″N/2°28′09.71″E	90.66	5	6.6	Very high	1970	378 ± 36	NA	79 ± 9
Cala d'Or	Mallorca	39°22′08.85″N/3°13′52.23″E	176.44	7	5.4	Very high	1970	389 ± 20	−0.026 ± 0.021	85 ± 8
Portocolom	Mallorca	39°25′02.56″N/3°16′01.53″E	139.35	9	4.9	High	1970	568 ± 41	−0.14 ± 0.09	94 ± 4
Sóller	Mallorca	39°47′40.05″N/2°41′06.48″E	185.45	11	1.2	High	1960	435 ± 72	NA	57 ± 16
Magalluf	Mallorca	39°30′13.46″N/2°32′38.35″E	166.69	6	0.2	High	1970	479 ± 35	−0.12 ± 0.03	60 ± 38
Es Port	Cabrera	39°08′45.41″N/2°56′42.21″E	6.73	17	−3.9	Moderately impacted	1991	227 ± 12	−0.06 ± 0.03	36.9 ± 1.9
Es Pujols	Formentera	38°43′42.16″N/1°27′17.78″E	187.06	4	−4	Moderately impacted	1970	969 ± 94	−0.04 ± 0.04	93 ± 4
Ses Illetes	Formentera	38°45′20.77″N/1°25′49.06″E	95.69	5	−6.5	Low	1970	556 ± 38	−0.05 ± 0.04	87.3 ± 0.3
Es Castell	Cabrera	39°09′09.93″N/2°55′49.93″E	0.46	5	−6.8	Low	1991	515 ± 39	−0.10 ± 0.05	81 ± 20
Sta.María	Cabrera	39°09′05.40″N/2°56′46.50″E	16.93	13	−6.8	Low	1991	470 ± 37	−0.100 ± 0.033	98 ± 2

P. oceanica meadows currently cover an approximate area of 650 km^2 around the archipelago of The Balearic Islands (Álvarez et al. 2015). Yearly surveys of permanent plots conducted in the meadows during the 3–11 yr before sampling demonstrate that most of the studied meadows had a similar shoot density (435 ± 72 to 643 ± 75 shoots m^{-2}) with the exception of Es Pujols in Formentera (969 ± 94 shoots m^{-2}), Cala d'Or (Mallorca, 389 ± 20 shoots m^{-2}), and Es Port (Cabrera National Park, 227 ± 12 shoots m^{-2}) (Table 1). In addition, *P. oceanica* net population growth in all meadows studied for the last decade was negative, indicating that their shoot density tended to decline during this period (Table 1).

Wave exposure

Wave exposure among sites was characterized by a fetch index, "the effective fetch" (Hakanson 1981), which is calculated from 15 distances (χ_i in km) between the study site and the opposite shore measured for every deviation angle γi from a central radius (0°) where γi equals 0°, ± 6°, ± 12°, ± 18°, ± 24°, ± 30°, ± 36°, and ± 42°. The central radius is placed in the direction where the opposite shore is located at the largest distance (Supporting Information Fig. SI1). The effective fetch (L_f) is then calculated using the Eq. 1.

$$L_f = (\Sigma\chi_i \cos \gamma i)/(\Sigma \cos \gamma i) \qquad (1)$$

Human pressure

Taking into account the specific context of the region of study we chose eight indicators of human activity to characterize the level of human pressure in the selected meadows (Supporting Information Table SI 1): human population; number of hotel beds; the number of sewage pipes and uncontrolled punctual discharges to each bay within 1 km distance from each sampling site; number of ports, marinas and/or yacht clubs and the number of berths located in the same bay of each meadow; number of boats potentially sailing regularly in coastal waters of each site; and fish farming activity in the area.

In order to classify the meadows according to their level of human pressure, indicators of pressure were standardized following the Z-score scaling method (Milligan and Cooper 1988) where the values for each indicator were recalculated as (V - mean V)/s, being V the value of the indicator, and mean V and s the average value and the standard deviation, respectively, of the indicator considering all sites. Standardized values of each indicator were added per site to obtain a human pressure index per meadow (Table 1, Supporting Information Table SI 1). According to the human pressure index obtained, meadows were classified across four different categories of human pressure: Low (sum < −5), Moderate (sum = −5 - 0), High (sum = 0 - 5), and Very high (> 5) (Table 1, Supporting Information Table SI 1). The spatial gradient of chlorophyll *a* (Chl *a*) concentration across the studied meadows agrees with the gradient of human pressure

defined, as Chl *a* concentration tends to increase from meadows under low to high and very high human pressure (Supporting Information Table SI 1).

We identified the onset of human pressure boom at each site as the year when the temporal trend of the cumulative number of hotel beds from 1931 to 2010 visually showed the first rapid increase (Supporting Information Fig. SI 2; Table 1). We support this date with that of the construction of the first yacht club or marina in the area (Supporting Information Fig. SI 2). For Ses Illetes, a non-urbanized area in Formentera and yet one of the top touristic spots in the island for which visitors influx records are not available, we assumed a similar date of human pressure increase as for Es Pujols (Supporting Information Fig. SI 2). We considered that human pressure started increasing at Cabrera sites the year when it was declared National Park (1991), when visitors were first allowed in the island. Hence, the year when human pressure started to rise (year$_{HP}$) at the studied sites ranged between 1960 and 1991 (Table 1). The periods considered before and after the year of the onset of human pressure (year $_{HP}$) at each site, respectively, encompassed from 1900 to year $_{HP}$ and from year $_{HP}$ to sampling year.

Sediment sampling and analyses

Seagrass meadows were sampled in June 2012, except Santa Maria that was sampled in June 2013. Three sediment cores were extracted from each meadow by hammering 60 cm long and 9 cm diameter PVC tubes into a maximum sediment depth ranging between 23 cm in Ses Illetes and 45 cm in Sta. Maria (Table 2). The compression of the sediment due to sampling was estimated in nine of the meadows and varied between 5% ± 3% in Es Pujols and 38% ± 4% in Es Castell (Table 2). The compression factor was used to correct the thickness of sediment layers to estimate the carbon stocks (g C_{org} cm^{-2}) assuming a linear sediment compression along the core depth during sampling and distributing the spatial discordances proportionally between the expected and the observed sediment column layer, as done in previous studies (Serrano et al. 2014).

One core per site was sliced at 1 cm intervals and was used for sediment grain size (Ø) and for estimating sediment accumulation rates through ^{210}Pb concentration analysis. Grain size analysis was performed at Universitat de Barcelona on a Beckman Coulter LS GB500. The sediment was classified according to the Udden-Wentworth grain size scale (Ø: < 4 μm, clay; Ø: 4–63 μm, silt; Ø: 63–2000 μm, sand and Ø: 2000–4000 μm, gravel).

Sediment accumulation rates were obtained from concentration profiles of ^{210}Pb, determined by alpha spectrometry through the measurement of its granddaughter ^{210}Po, assuming radioactive equilibrium between both radionuclides. About 100–200 mg aliquots of each sample were spiked with ^{209}Po and microwave digested with a mixture of concentrated HNO$_3$ and HF. Boric acid was then added to complex

Table 2. Number of cores, maximum sediment depth sampled and estimated core compression during sampling, mean sediment grain size ($\pm$ SE) (and the depth of the core used for granulometric analyses) and the observed depth and year ($\pm$ SE) of the oldest sediment layer accumulated since 1900 (oldest age) estimated from ^{210}Pb dating techniques in one core per site.

| Station | | Sampling | | Granulometry | | [210]Pb dating | |
	N cores	Max. core length (cm)	Compression % (mean ± SE)	Grain size (μm, mean ± SE)	Depth (cm)	Oldest age (mean ± SE)	Depth (cm)
Pollença	3	39	35 ± 4	203 ± 12	37	1912 ± 3	17
Sta.Ponça	3	34	NA	547 ± 23	32	1918 ± 7	19
Cala d'Or	3	32	17 ± 3	535 ± 18	32	1930 ± 1	21
Portocolom	3	35	21 ± 7	545 ± 24	27	1906 ± 7	29
Sóller	3	39	NA	1026 ± 141	37		
Magalluf	3	43	13 ± 2	648 ± 39	41	1912 ± 4	15
Es Port	3	36	31 ± 3	338 ± 24	35	1918 ± 4	17
Es Pujols	3	27	5 ± 3	367 ± 15	15		
Ses Illetes	3	23	11 ± 4	547 ± 33	21		
Es Castell	3	35	38 ± 4	315 ± 10	33	1921 ± 9	17
Sta.Maria	4	45	20 ± 3	550 ± 16	27	1943 ± 2	13

fluorides. The resulting solutions were evaporated and diluted to 100 mL 1M HCl and Po isotopes were autoplated onto pure silver disks. Polonium emissions were measured by alpha spectrometry using PIPS detectors (CANBERRA, Mod. PD-450.18 A.M). Reagent blanks were comparable to the detector backgrounds (i.e., $1\text{--}2 \times 10^{-5}$ c s^{-1}). Analyses of replicate samples and reference materials were carried out systematically to ensure the accuracy and the precision of the results. The supported ^{210}Pb was estimated as the average ^{210}Pb concentration of the deepest layers once ^{210}Pb reached constant values. Then, excess ^{210}Pb concentrations were obtained by subtracting the supported ^{210}Pb from the total [210]Pb. Age models of the sediment records were obtained by modeling the excess ^{210}Pb concentration profiles along the accumulated mass at each site. The age of the sediment layers along the core profiles was estimated using the Constant Rate of Supply model (CRS, Appleby and Oldfield 1978), except for Cala d'Or and Porto Colom that did not fulfill the requisites for the application of the CRS model (i.e., in Cala d'Or supported ^{210}Pb was not reached and in Porto Colom the flux of excess ^{210}Pb to the sediment was not constant through time). These sediments were dated by means of the Constant Flux: Constant Sedimentation model (CF:CS, Krishnaswamy et al. 1971).

The remaining portions of the dated cores together with the other additional cores per site, sliced at 2 cm intervals, were used to determine sediment density and sediment organic matter concentration (OM, in %DW). Sediment density was estimated as the ratio between the sediment sample dry weight (g) (dried at 60°C during a minimum of 48 h) and the sample fresh volume (cm^3). OM (%DW) was estimated as the fractional weight loss of dry sediment in the samples after combustion at 550°C for 4 h. In addition, the

sediment organic carbon concentration (C_{org}, in %DW) was analyzed in alternate 2 cm slices from one core per site on an Elemental Analyser - Isotope Ratio Mass Spectrometry (EA-IRMS) at Iso-Analytical Laboratory (United Kingdom). The relationship between OM (%DW) and C_{org} (%DW) contents measured in the same sample ($n = 101$, Supporting Information Fig. SI 3), described by the fitted regression Eq. 2, was used to estimate C_{org} in those samples analyzed for OM only:

$$C_{org} = -0.601 \ (\pm 0.090) + 0.290 \ (\pm 0.009)$$
$$OM \ (F_{100} = 973.8, R^2 = 0.91, \ p < 0.001) \tag{2}$$

The density of C_{org} (g C_{org} cm^{-3}) along the sediment profile was estimated as the product of % C_{org} by the sediment density of each sediment slice, divided by 100.

Carbon stocks and burial rates estimation

The C_{org} stock (g C_{org} cm^{-2}) along the sediment profile was estimated as the product of the C_{org} density (g C_{org} cm^{-3}) by the sediment slice decompressed thickness.

We estimated carbon stocks for the sediment top-30 cm by multiplying the average C_{org} stocks per slice (g C_{org} cm^{-2}) for a minimum of three replicated cores per station, within the top-30 cm of the sediment, by 30. The reported C_{org} stocks (kg C_{org} m^{-2}) correspond to decompressed stocks (as explained above), except for two meadows where sediment compression could not be measured during sampling (Sóller and Sta. Ponça). To compare with global estimates we extrapolate top-30 cm C_{org} stocks (observed and decompressed) to a 1-m depth and to a one-hectare scale (Supporting Information Table SI 4) taking into account data on meadow surface cover (%) per site (Table 1). Extrapolation to 1-m depth is supported by the fact that, as

shown in the results, no general trend in C_{org} concentration (%DW) with sediment depth among the meadows examined was found.

Average C_{org} burial rates (g C_{org} m^{-2} yr^{-1}) at each station were calculated for different periods (i.e., since 1900, before and after the increase of human pressure) using the data on accumulated stocks of C_{org} (g C_{org} cm^{-2}) during each period, identified by the ^{210}Pb derived-chronology, divided by the number of years of each period. The temporal variability in the C_{org} burial was examined calculating the ratio of burial rates after and before the onset of the increase of human pressure, with values below or above 1 denoting a decrease or an increase in the C_{org} burial after the onset of anthropogenic pressure increase.

To estimate the C_{org} stocks accumulated between 1900 and present we multiplied the estimated average C_{org} burial rate since 1900 by the number of years until sampling was conducted (112 for all the meadows except for Sta. Maria which was 113).

An overestimation of the carbon buried in the most recent period compared to that stored in the period before may occur if a potential remineralization of the sediment organic matter along time is not considered. In order to assess the magnitude of this error, we estimate recent C_{org} stocks and burial rates after decomposition during a number of years equivalent to the age difference between the two periods examined. We did so by considering the highest available decay rate of organic matter buried in *P. oceanica* sediments (-0.0005 yr^{-1}, Serrano et al. 2012) and applying the most commonly used equation in the literature on seagrass tissue decomposition (Enriquez et al. 1993; Pergent et al. 1994; Serrano et al. 2012)

$$W_t = W_o \cdot e^{-\lambda t} \qquad (3)$$

where W_t is the predicted C_{org} stock, W_o is the observed C_{org} for the most recent period, λ is the decay rate (0.0005 yr^{-1}) and t is the difference between the average age of the sediment accumulated during the periods after and before the anthropogenic pressure increase.

Statistical analyses

One-way ANOVA test was used for determining significant differences in average mean grain size and C_{org} concentration along the whole core profiles and top meter stocks (decompressed) between stations. A post-hoc Tukey test was used to identify the sites with significantly different C_{org} stocks. Wilcoxon Signed rank test was used to assess the difference in the C_{org} burial rates between the periods before and after the anthropogenic pressure increased. Linear regression analysis was used to assess the change of C_{org} (%DW) with sediment depth, the effect of fetch on the mean sediment grain size and the effect of water depth, fetch and human pressure index on the C_{org} burial rates.

Propagated standard errors (SE) were calculated for the top-30 cm stocks and C_{org} burial rates taking into account the SE associated to sediment age and that derived from C_{org} stocks of three replicate cores per site (Supporting Information).

Results

Sediments were dominated by the sand fraction (Ø: 63–2000 μm), which represented an average ($\pm$ SE) of 84% $\pm$ 1% of the seagrass sediments examined. However, there were significant differences in the mean grain size (ANOVA, $F_{229} = 23.6$, $p < 0.0001$; Table 2) and in the contribution of different grain size fractions between sites (Supporting Information Fig. SI 4). The sediments from Sóller had the largest mean grain size, followed by those from Magalluf, whereas those from Pollença and Es Port were characterized by presenting the largest proportion of silt and clay fractions (Supporting Information Fig. SI 4).

The concentration of sediment C_{org} (%DW) in the *P. oceanica* meadows studied averaged ($\pm$ SE) 1.8 $\pm$ 0.5 C_{org} (%DW) and showed significant differences between meadows (ANOVA, $F_{780} = 112$, $p < 0.0001$), ranging from a minimum average concentration of 0.7 $\pm$ 0.3 C_{org} (%DW) in Es Castell to a maximum of 5.8 $\pm$ 0.5 C_{org} (%DW) in Pollença. C_{org} (%DW) significantly changed along the sediment depth profile in 6 of the 11 meadows examined, decreasing with depth at average rates of -0.08 ± 0.02 (%DW) cm^{-1}, -0.040 ± 0.005 (%DW) cm^{-1}, -0.050 ± 0.009 (%DW) cm^{-1} and -0.03 ± 0.01 (%DW) cm^{-1} in Es Pujols, Es Port, Porto Colom and Sta. Ponça, respectively, and increasing with sediment depth at average rates of 0.03 $\pm$ 0.005 C_{org} (%DW) cm^{-1} and 0.014 $\pm$ 0.004 C_{org} (%DW) cm^{-1} in Magalluf and Sóller, respectively (Fig. 2; Supporting Information Table SI 2).

The average ($\pm$ SE) carbon stock stored in the top-30 cm sediments of the meadows examined was estimated as 6.1 $\pm$ 1.4 kg C_{org} m^{-2}, with significant differences between stations (ANOVA, $F_{129} = 54.58$, $p < 0.0001$), ranging from a minimum of 1.94 $\pm$ 0.41 kg C_{org} m^{-2} in Es Castell to a maximum of 11.3 $\pm$ 1.2 kg C_{org} m^{-2} in Pollença (Fig. 3). The two meadows for which decompressed stocks could not be estimated (Sta. Ponça and Sóller) are not included in the statistical analyses.

Total ^{210}Pb concentrations showed a clear decline with depth in 8 out of the 11 sites (Supporting Information Fig. SI 5). Excess ^{210}Pb was not detected (or very limitedly) in sediment cores collected at Sóller and Ses Illetes and evidenced intense mixing in Es Pujols, precluding the determination of reliable sediment chronologies at these sites.

Meadows where sediments could be dated ($n = 8$) accumulated on average 3.0 $\pm$ 0.7 kg C_{org} m^{-2} between years 1900 and 2012, with an average C_{org} burial rate of 26 $\pm$ 6 g C_{org} m^{-2} yr^{-1}. However, the C_{org} buried in *P. oceanica* meadows since 1900 widely varied across sites, ranging from 1.0 $\pm$ 0.2 kg C_{org} m^{-2} in Magalluf to 5.9 $\pm$ 0.3 kg C_{org} m^{-2} in
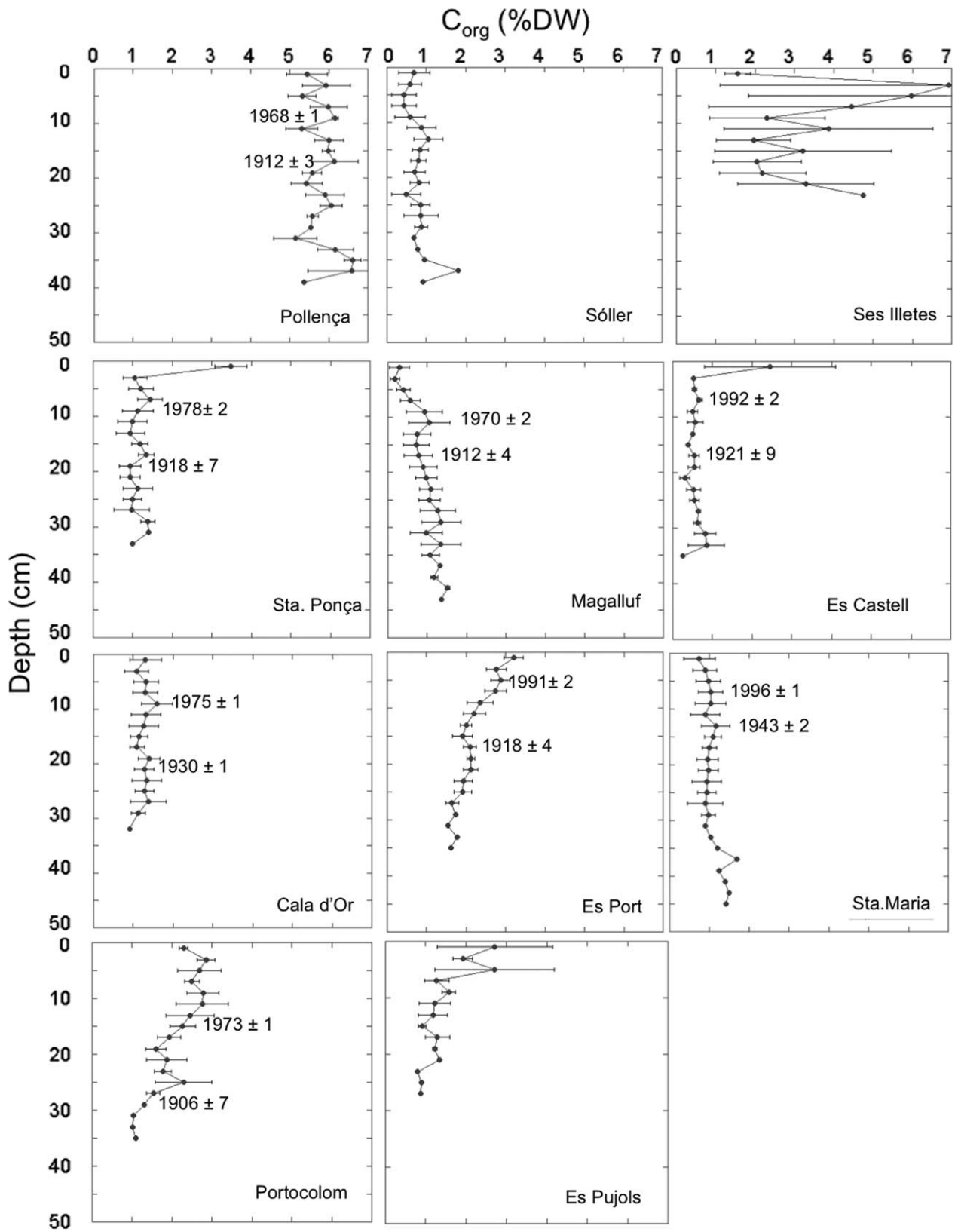
Fig. 2. Average (± SE) organic carbon concentration (C$_{org}$ %DW) of a minimum of three cores per meadow along the observed depth profile. The years (± SE) of deposition of the oldest sediment layer accumulated since 1900 and since the onset of increase in human pressure are indicated.
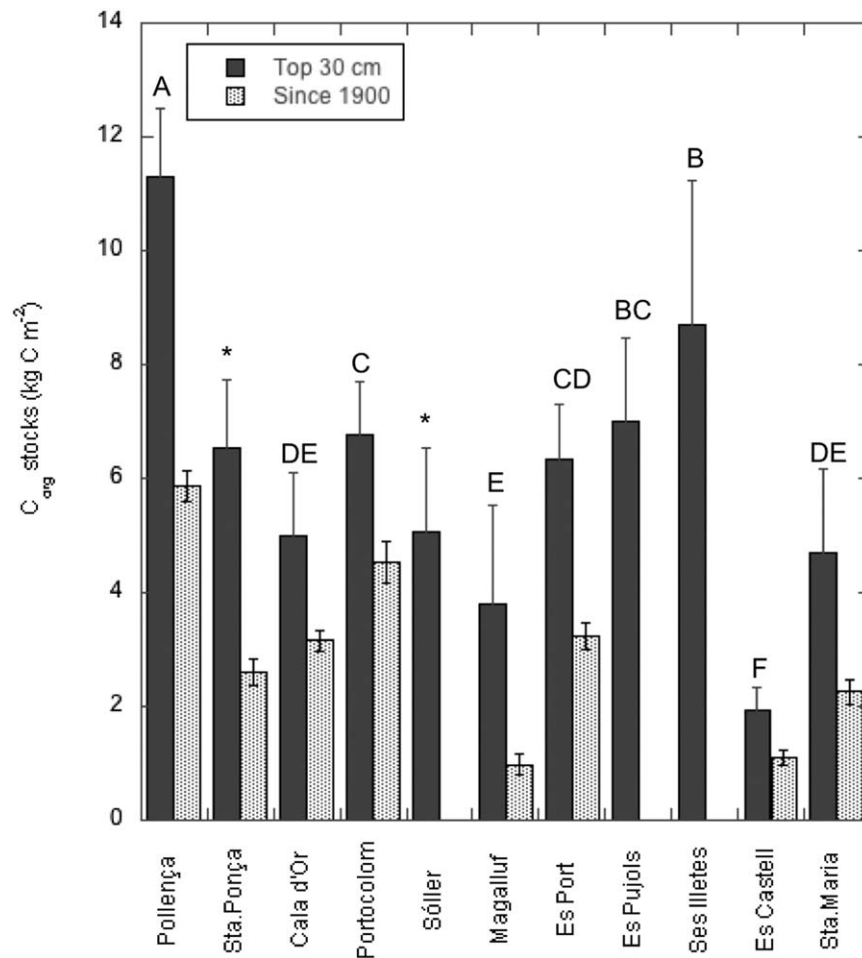
Fig. 3. Mean ± SE organic carbon (C_{org}) stocks (kg C m^{-2}) stored in the sediments top-30 cm and since 1900 for the *P. oceanica* meadows studied. Different letters indicate significant differences in the top-30 cm carbon stocks (ANOVA, $F_{129} = 54.58$, $p < 0.0001$; Tuckey-Kramer test, $\alpha = 0.05$). The asterisk (*) identifies those meadows for which decompressed stocks are not available and observed stocks are represented but not included in the statistical analyses.

Pollença (Fig. 3), with corresponding average burial rates ranging from 9 ± 2 g C_{org} m^{-2} yr^{-1} in Magalluf to 52 ± 2 g C_{org} m^{-2} yr^{-1} in Pollença (Table 3).

The effective fetch in the meadows examined ranged from 0.46 km in Es Castell, an enclosed bay, to 187 km in Es Pujols, a highly exposed site (Table 1). Sediment grain size in the seagrass examined increased significantly with increasing fetch (linear regression analysis: $F_{229} = 81.9$, $R^2 = 0.26$, $p < 0.0001$; Supporting Information Fig. SI 6).

On the contrary, there was no significant relationship between water depth, effective fetch or human pressure index and the average C_{org} burial rates since 1900 across meadows (Fig. 4a–c) ($p > 0.05$). Yet, C_{org} burial rates in sheltered (fetch < 20 km) meadows increased significantly with increasing human pressure ($R^2 = 0.9$; $p < 0.05$) whereas no significant relationship was found across exposed meadows (fetch > 20 km; Supporting Information Fig. SI 7).

The C_{org} burial rate increased since the onset of the increase in human pressure in all the meadows examined

except for Magalluf and Cala d'Or (Fig. 5; Table 3). Considering all the studied meadows, the average C_{org} burial rate since acceleration of anthropogenic pressure (38 ± 9 g C_{org} m^{-2} yr^{-1}) was significantly higher than that recorded for the period before (26 ± 7 g C_{org} m^{-2} yr^{-1}) (Wilcoxon Signed rank test, df = 7, $S = -15$, $p = 0.039$). Correcting the estimates of C_{org} burial rates of the most recent period for the potential remineralization of the C_{org} stocks during the time span between the two periods, assuming a decomposition rate of *P. oceanica* carbon of 0.0005 yr^{-1} (Serrano et al. 2012), resulted in a reduction of the recent C_{org} burial rates of between 2.0% and 3.1% depending on the meadow (Supporting Information Table SI 3).

Discussion

The *P. oceanica* meadows studied here support relatively low C_{org} sinks compared to *P. oceanica* meadows studied in the past. Estimated top meter sediment stocks, observed and

Table 3. Organic carbon (C_{org}) burial rate (g C_{org} cm^{-2} yr^{-1}) since 1900 until present and for the periods before and after the approximate year of acceleration in human pressure at each station (Year$_{HP}$).

Station	Human pressure	Year$_{HP}$	Since 1900		Before Year$_{HP}$		After Year$_{HP}$	
			g C_{org} m^{-2} yr^{-1}	SE	g C_{org} m^{-2} yr^{-1}	SE	g C_{org} m^{-2} yr^{-1}	SE
Pollença	Very high	1960	52	2	58	5	65	4
Sta. Ponça	Very high	1970	23	2	22	4	33	3
Cala d'Or	Very high	1975	28	2	32	3	30	2
Portocolom	High	1970	40	3	30	4	64	4
Magalluf	High	1970	9	2	10	3	10	3
Es Port	Moderate	1991	29	2	30	3	42	6
Es Castell	Low	1991	10	1	8	1	21	3
Sta. Maria	Low	1991	20	2	18	3	43	6
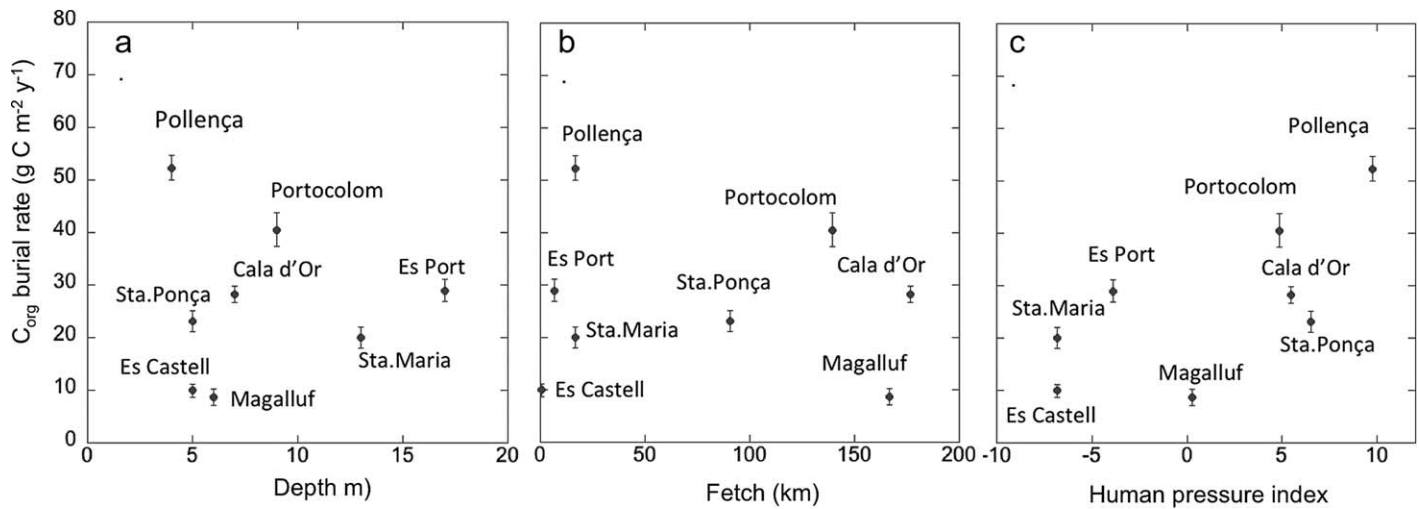
Fig. 4. Organic carbon (C_{org}) burial rate (g C m^{-2} yr^{-1}) since 1900 vs. (**a**) depth ($y = 26.8 \pm 12.2 - 0.05 \pm 1.32x$; $R^2 = 0.0002$, $p > 0.05$), (**b**) effective fetch ($y = 27.7 \pm 8.2 - 0.02 \pm 0.08x$; $R^2 = 0.007$, $p > 0.05$), and (**c**) human pressure index in the meadows studied ($y = 24.6 \pm 4.2 + 1.56 \pm 0.7x$; $R^2 = 0.5$, $p > 0.05$). See Methods for description of calculation of human pressure index.

decompressed (202 ± 79 Mg C_{org} ha^{-1} and 167 ± 65 Mg C_{org} ha^{-1}, respectively, Supporting Information Table SI 4) are around half those reported in previous studies (372 ± 75 Mg C_{org} ha^{-1}, Fourqurean et al. 2012) whereas burial rates (9–52 g C_{org} m^{-2} yr^{-1}) rank among the lowest values reported for other *P. oceanica* meadows studied in the past (6–175 g C_{org} m^{-2} yr^{-1}, Mateo et al. 1997). These results suggest that data hitherto available may have been biased toward meadows supporting very high carbon stocks and burial rates, as sampling was largely directed to *P. oceanica* reefs (e.g., Mateo et al. 1997; Serrano et al. 2012) that are impressive structures that can reach several meters high (Lo Iacono et al. 2008) but may not be representative of the whole spectrum of existing *P. oceanica* meadows.

Despite the studied seagrass meadows occur at depths that encompass up to 13 m difference, variability in carbon burial rates was uncoupled to that of water depth (Fig. 4a). Hence, our results do not support the recent findings pointing out

that seagrass carbon burial capacity decreases with increasing water depth as a consequence of the decrease of seagrass productivity (Serrano et al. 2014). In fact, carbon burial in seagrass meadows also depends on the accumulation of allochthonous carbon, that has been demonstrated to contribute up to a 50% of the total C_{org} buried in the top seagrass sediments (Kennedy et al. 2010). The loading of allochthonous carbon in the water column depends on local factors, and is usually higher in coastal areas influenced by river discharges and/or nearby urbanized areas (Short and Burdick 1996; Bowen and Valiela 2001). On the other hand, C_{org} burial might increase in deeper meadows, due to a reduction in water flow, that enhances sedimentation and decreases resuspension and sediment aeration, preventing organic matter remineralization (Lavery et al. 2013). Therefore, the effect of water depth in seagrass C_{org} burial is still unclear and further research is needed taking into account the different local conditions such as the different sources of carbon to seagrass meadows.
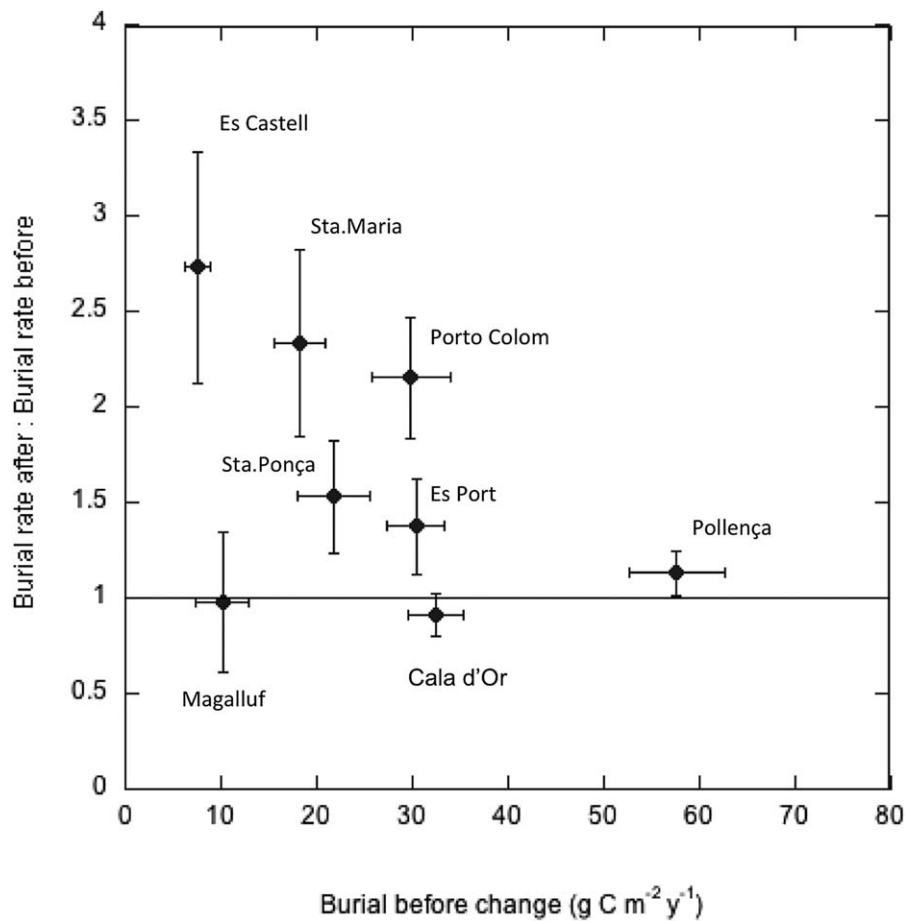
Fig. 5. Relationship between organic carbon (C_{org}) burial rate ($\pm$ SE) per meadow for the period between 1900 and the onset of human pressure increase (*x* axis) and the ratio ($\pm$ SE) between the C_{org} burial rates for the periods after and before the year of increase of human pressure (*y* axis) in each of the meadows studied. The transition dates between both periods are reported in Table 1.

Mean grain size tended to increase with fetch (Supporting Information Fig. SI 6), consistent with previous studies conducted with other species (Murphey and Fonseca 1995; Fonseca and Bell 1998). This result demonstrates the suitability of the fetch index used to represent the hydrodynamic conditions of the different sites and the relevance this factor has in affecting sedimentary processes in seagrass meadows. Hydrodynamic forcing was also expected to control the C_{org} burial rates as more sheltered environments would favor the sedimentation of allochthonous carbon in seagrass meadows while reducing export of the carbon produced by the meadow and the erosion of the sediment carbon deposits. However, this expectation was not fully supported by the results obtained. Although the highest C_{org} burial rate was found in one of the most sheltered meadows (Pollença, 52 ± 3 g C m^{-2} yr^{-1} with fetch = 17 km) and the lowest burial rate was found in one of the most exposed sites (Magalluf, 9 ± 2 g C m^{-2} yr^{-1} and fetch= 167 km) some sheltered meadows showed very low C_{org} burial rates, such as those in Es Castell and Santa Maria (10 ± 2 and 20 ± 2 g C m^{-2} yr^{-1} with fetch equal to

0.5 km and 16 km, respectively) and some other meadows with medium and high exposure showed high burial rates, such as Portocolom or Cala d'Or (40 ± 3 and 28 ± 2 g C m^{-2} yr^{-1} with fetch = 139 and 176 km, respectively).

C_{org} burial rates tended to increase from pristine locations (9 ± 2 g C_{org} m^{-2} yr^{-1}) to meadows supporting "very high" human pressure (35 ± 9 g C_{org} m^{-2} yr^{-1}, Fig. 4c; Table 3) but this relationship was only significant for sheltered locations (Supporting Information Fig. SI 7). Moreover, the average C_{org} burial in the *P. oceanica* meadows examined significantly increased (by $69\% \pm 24\%$) since the onset of increase in human pressure in coastal areas. The observed increase in C_{org} burial rates toward present could be partially attributable to the different time for diagenetic removal of carbon stocks among the two periods compared. However, the decomposition of organic matter accumulated in sediments is usually reflected in a decay in carbon concentration along the sediment depth profile (Garten et al. 2007) and, in this study, such decay in carbon concentration with increasing sediment depth was observed only in three out of the six

meadows where C_{org} burial rate significantly increased toward present. In addition, the potential remineralization of the most recent accumulated C_{org} stocks at a decay rate of 0.0005 yr^{-1}, (Serrano et al. 2012), for a period of time equal to the age difference of the stocks accumulated during the high and low human pressure periods considered, would lead to an apparent reduction of the recent C_{org} burial rates of between 2.0% and 3.1%, depending on the meadow (Supporting Information Table SI 3). This apparent reduction (2.0–3.1%) in the recent C_{org} burial rates due to remineralization is much lower than the average increase (69% ± 24%) in the C_{org} burial observed between periods. Hence, the general increase in C_{org} burial rates toward present along with the spatial variability observed in the C_{org} burial rates among the meadows examined suggest that human pressure leads to higher C_{org} burial rates within the region of study.

Several hypotheses might be offered to explain these results. Carbon burial in seagrass meadows depends on plant productivity (e.g., shoot density) and the presence of allochthonous subsidies for sedimentation and burial in the sediment. As human pressure increases, the input of nutrients into coastal waters is enhanced (Short and Burdick 1996; Bowen and Valiela 2001; Nedwell et al. 2002). Nutrient enrichment during the last decades may have had a fertilization effect and led to an increase in plant biomass productivity, especially in those areas highly influenced by human activity. However, plant biomass does not seem to explain the differences in the C_{org} burial rates found among meadows and the general increase observed toward present. Shoot densities of the meadows showing the highest burial rates (643 ± 75 and 568 ± 41 shoots m^{-2} in Pollença and Portocolom, respectively) have not been significantly different from those found in the meadows showing the lowest C_{org} burial rates (Es Castell and Magalluf with 515 ± 40 and 479 ± 35 shoots m^{-2}, respectively) (Table 1) and the shoot population growth rate in the meadows examined has been declining for, at least, the last 3–11 yr (Table 1).

On the other hand, an excess input of nutrients in coastal waters usually enhances eutrophication (Nixon 1995) and the increase in the load of allocthonous carbon in the water column that sinks and accumulates in the sediment. The load of allochthonous carbon in the water column is likely to differ among the different meadows according to their level of anthropogenic pressure (Bowen and Valiela 2001), being lower in pristine meadows compared to those under a relatively higher human pressure (as supported by data on Chl *a* shown in Supporting Information Table SI 1), particularly so for the past decades, where human pressure has been greatest. Indeed, the second highest C_{org} burial rate in this study (40 ± 3 g C_{org} m^{-2} yr^{-1}) was observed in the sediments from Portocolom, where a higher C_{org} sedimentation rate compared to other meadows (i.e., Sta. Maria and Magalluf) has been reported in the past due to high nutrient and organic inputs from the surrounding town, boating activity

and a fish farm (Holmer et al. 2004; Vaquer-Sunyer et al. 2012). Symptoms of eutrophication have been observed in Es Port bay during the summer period (Marbà et al. 2006; Supporting Information Table SI 1) where sedimentation rates exceeded those measured at the pristine meadows elsewhere in Cabrera National Park (e.g., Sta. Maria) (Supporting Information Table SI 2; Holmer et al. 2004). In addition, an increase in the accumulation of allochthonous carbon in coastal sediments as a consequence of human pressure increase has been already reported in previous studies (Savage et al. 2010), including studies conducted in seagrass meadows (Macreadie et al. 2012). Hence, we hypothesize that the higher C_{org} burial rates identified in meadows under a high human pressure and the general increase in the C_{org} burial rates since the onset of human pressure in the region studied are explained by an increased load of allochthonous carbon in the water column resulting from enhanced eutrophication. Yet, the magnitude of the deposition of this allochthonous carbon and, therefore, the effect of human pressure on C_{org} burial rates, is likely constrained by fetch, being enhanced in sheltered meadows, with extended seawater residence time (e.g., Es Port and Pollença), and prevented in highly exposed sites, such as Magalluf and Cala d'Or, that despite supporting "high" and "very high" human pressure showed relatively low and medium C_{org} accumulation rates, respectively, since 1900 and since the onset of human pressure (Table 3). The examination of the relationship between C_{org} burial rates and human pressure in sheltered (fetch < 20 km) and exposed (fetch > 20 km) meadows separately supports this hypothesis (Supporting Information Fig. SI 7).

Unfortunately, the shorter time period of meadow demographic observations (3–11 yr) compared to that encompassed by the sediment record for the most recent period ($\sim$ 21–52 yr) and the absence of long-term time series of Chl *a* concentration in the water column at the study sites limit the assessment of the role that trajectories of meadow demographic characteristics and allochthonous carbon abundance may have on *P. oceanica* carbon sinks.

In summary, our study contributes to the data available on C_{org} sinks in *P. oceanica* meadows, provides C_{org} burial rates in seagrass meadows during the last century, a period of an intense increase in human pressure in coastal environments, and explores the effect of water depth and wave exposure (fetch). No effect of water depth on C_{org} burial was found and although fetch clearly controlled sedimentation patterns in the meadows examined, it was not enough to explain differences in C_{org} burial rates. Carbon burial rates tended to be higher in meadows under a relatively higher anthropogenic pressure and to rise during the period after human pressure increased in each site. The possible eutrophication associated to the increase of human pressure on coastal areas may have enhanced the contribution of allochthonous carbon to the sediment stocks, particularly so

in sheltered meadows (i.e., low fetch). However, this hypothesis needs to be further explored to consider other mechanisms that may explain the observed increase in C_{org} burial rate.

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Conflict of Interest

None declared.