LIMNOLOGY
and
OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 00, 2017, 00–00

doi: 10.1002/lno.10509

Dynamics of carbon sources supporting burial in seagrass sediments under increasing anthropogenic pressure

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Abstract

Seagrass meadows are strong coastal carbon sinks of autochthonous and allochthonous carbon. The aim of this study was to assess the effect of coastal anthropogenic pressure on the variability of carbon sources in seagrass carbon sinks during the last 150 yr. We did so by examining the composition of the sediment organic carbon (C_{org}) stocks by measuring the $\delta^{13}C_{org}$ signature and C : N ratio in ^{210}Pb dated sediments of 11 *Posidonia oceanica* seagrass meadows around the Balearic Islands (Spain, Western Mediterranean) under different levels of human pressure. On average, the top meter sediment carbon deposits were mainly (59% ± 12%) composed by *P. oceanica* derived carbon whereas seston contribution was generally lower (41% ± 8%). The contribution of *P. oceanica* to the total sediment carbon stock was the highest (~ 80%) in the most pristine sites whereas the sestonic contribution was the highest (~ 40–80%) in the meadows located in areas under moderate to very high human pressure. Furthermore, an increase in the contribution of sestonic carbon and a decrease in that of seagrass derived carbon toward present was observed in most of the meadows examined, coincident with the onset of the tourism industry development and coastal urbanization in the region. Our results demonstrate a general increase of total carbon accumulation rate in *P. oceanica* sediments during the last century, mainly driven by the increase in sestonic C_{org} carbon burial, which may have important implications in the long-term carbon sink capacity of the seagrass meadows in the region examined.

Mounting evidence of the capacity of seagrass meadows to capture and store significant amounts of carbon (e.g., Mateo and Romero 1997; Kennedy et al. 2010; Duarte et al. 2013) ranked these ecosystems among the most important organic carbon (C_{org}) sinks on Earth (Duarte et al. 2005; Nellemann et al. 2009; Mcleod et al. 2011; Lavery et al. 2013) with estimated global C_{org} burial rates comparable to those for saltmarshes, mangroves, and terrestrial forests (Mcleod et al. 2011). Due to the high global loss rate of seagrass meadows (Waycott et al. 2009), protection and conservation actions to preserve seagrass carbon sinks have become a relevant component of strategies to mitigate climate change, termed "Blue Carbon" strategies (Laffoley and Grimsditch 2009; Nellemann et al. 2009; Duarte et al. 2013).

Kennedy et al. (2010) estimated, based on a synthesis of stable carbon isotopes in seagrass sediments, that around 50% of the C_{org} stored in the top 10 cm of seagrass sediments is derived from seagrass biomass, although a wide variability was found between sites (with 25th and 75th percentiles equivalent to 33% and 62% contributions, respectively). The remaining sediment carbon was of allochthonous origin derived from phytoplankton and/or terrestrial inputs, which is trapped into seagrass sediment due to the effective role of seagrass canopies as filters of sestonic particles (Gacia et al. 2002; Bos et al. 2007; Hendriks et al. 2010). The identification of the sources of C_{org} and their contribution to the sedimentary sink is especially relevant as these sources differ in their persistence in the sediment stock (Holmer et al. 2004). Sestonic matter,

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particularly phytoplankton, is much more labile than seagrass tissues (Enriquez et al. 1993) as reflected in much faster decomposition rates (K, median $K_{seagrass} = 0.007$ d^{-1}, $K_{microalgae} = 0.046$ d^{-1}; Enriquez et al. 1993). Therefore, carbon deposits enriched in seston are expected to be more prone to microbial decomposition, conducive to a lower burial efficiency and to the release of much of the sediment C_{org} back to the ocean-atmosphere CO_2 pool. Furthermore, the remineralization of sediment C_{org} may affect seagrass growth and survival by increasing nutrient availability, which enhances seagrass growth in nutrient limited environments, or/and by supporting high sulfate reduction rates (SSR) that may lead to anoxic conditions (Holmer and Kristensen 1996) that compromise seagrass survival (Calleja et al. 2007). Therefore, assessments of seagrass carbon sinks should not only focus on the total C_{org} deposited but also on the sources of the C_{org} being stored.

A requirement for atmospheric CO_2 sinks to be relevant to climate change mitigation is that the C removed must not return to the atmosphere as CO_2 over time scales longer than approximately 40–150 yr (Dobes et al. 1998; Tipper and Jong 1998; Marland et al. 2001). Seagrass C_{org} has been shown to remain in the sediment deposits over millenary scales (e.g., Mateo et al. 1997) but, since the Industrial Revolution seagrass meadows have experienced major changes due to multiple drivers, including direct impacts from human modification of watersheds and coastal areas, pollution, and anthropogenic climate change (Duarte 2014) that may have altered their C sink capacity for the last century. Eutrophication for instance, usually associated with an increase in human pressure in coastal areas, is the main cause of the widespread decline of seagrass meadows worldwide (Waycott et al. 2009). While seagrass decline with eutrophication is likely to result in a reduced input of seagrass-derived C_{org} to seagrass sediments, the enhanced phytoplankton production is expected to lead to an increased input of seston-derived C_{org} to seagrass sediments (Bowen and Valiela 2001). Hence, the contribution of different carbon sources to sediment C_{org} sinks is expected to differ among seagrass meadows under different levels of human pressure, due to different meadow health status and/or loads of sestonic carbon in the water column. It is also expected that the relative contribution of carbon sources to C_{org} stocks has varied over time, provided the major global increase in anthropogenic pressure that coastal areas have experienced over the past 60 yr (Duarte 2014).

Here, we assess the sources of C_{org} to dated sediment deposits in *Posidonia oceanica* seagrass meadows during the last 150 yr with the aim of resolving the variability among meadows and over time in response to the extent and increase of anthropogenic pressures on the coastal areas. This work is carried out in The Balearic Islands (Western Mediterranean), one of the most important touristic destinations in Europe (Hof and Schmitt 2011) where the development of the touristic industry around the 60s led to a dramatic increase in the population density and urbanization in the coastal areas, with subsequent deterioration of the water quality (Morey et al. 1992; Hof and Schmitt 2011; Roig-Munar et al. 2013). The anthropogenic pressure varies from low at near-pristine, protected and undeveloped sites to very high at strongly human-influenced bays where long water residence time likely amplifies anthropogenic impacts in the coastal ecosystems (Marbà et al. 2002; Garcia-Solsona et al. 2010). *P. oceanica* meadows, a key ecosystem endemic to the Mediterranean Sea, are remarkable in that they support the highest carbon burial rates and sedimentary C_{org} stocks yet reported for any seagrass species (Fourqurean et al. 2012; Lavery et al. 2013). The seagrass meadows around the Balearic Islands are extensive, covering an estimated area of 633 km^2 extending down to 45 m depth (Álvarez et al. 2015). However *P. oceanica* meadows have been declining in this region for at least the last two decades due to the increase in human pressures and water temperature (Marbà and Duarte 2010; Marbà et al. 2014).

We hypothesize that the contribution of different carbon sources to the sediment deposits in the meadows examined will vary depending on exposure to coastal anthropogenic pressures, and specifically, that the contribution of sestonic-derived carbon will increase with increasing human influence in the coastal areas studied.

Methods

Study sites

The sources of buried carbon were assessed in a total of 11 *P. oceanica* meadows in the Balearic Islands: 6 in Mallorca Island, 2 in Formentera Island, and 3 in the Cabrera Archipelago National Park (Fig. 1). Mallorca is the largest and most populated island, with about 50% of its territory transformed by human activities (Balaguer et al. 2008). All meadows from Mallorca selected for this study are under a significant level of human pressure derived from a high urbanization and/or nautical activities. Formentera is the smallest and least populated island of the archipelago. Although there are still some non-urbanized areas (e.g., Ses Illetes beach), its rise as an important touristic destination, with particularly intense pressure from nautical tourism, led to a rapid urbanization of certain sites (e.g., Es Pujols) and to a significant degradation of the coastal areas (Morey et al. 1992; Roig-Munar et al. 2013). The Cabrera Archipelago is a group of small islands that were used as an army station from 1940 until its declaration as a National Park in 1991. Although Cabrera Archipelago does not support resident population, it receives a relatively intense flow of visitors. Santa Maria bay, closed to visitors since 1993, and Es Castell, where anchoring is not allowed, can be considered, along with Ses Illetes (in Formentera) the pristine *P. oceanica* meadows sampled in this study. On the contrary, the meadow at

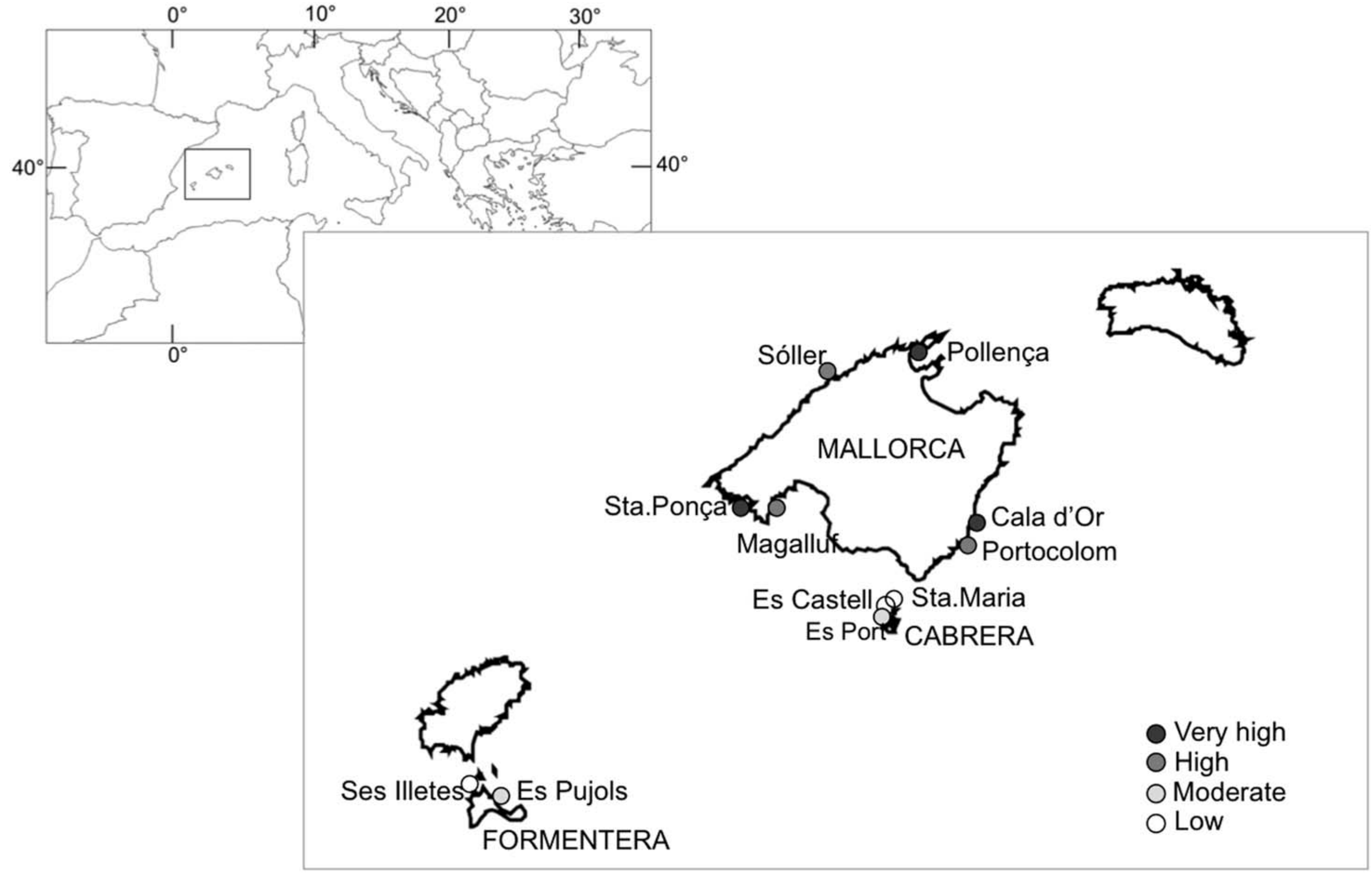

Fig. 1. Sampling sites in the Balearic Islands. Symbol color gradient indicates the level of human pressure in each site, from "low" to "very high."

Es Port's bay supports a higher level of human pressure, as contains the main services of the park, receives the visitors arriving by ferries and it is the only location in the park where sailing boats are allowed to overnight in one of the 50 buoys available. The sewage produced by visitors in moored ships, few of which are equipped with holding tanks, is usually released raw to Es Port water along with the outflow of the treated sewage from land (PNMTAC 2009).

Based on the quantification of several indicators of anthropogenic pressure in coastal areas such as population, number of hotel beds, nautical activity (ports, berths and boats potentially sailing regularly in coastal waters), sewage outfalls, uncontrolled punctual discharges, and fish farming activities, the meadows selected were assigned to each of four different categories of human pressure (Mazarrasa et al. 2017), ranging from "Low" pressure for the three most pristine sites of the study (Ses Illetes in Formentera and Es Castell and Sta. Maria in Cabrera National Park) to "Moderate" pressure (i.e., Es Pujols in Formentera and in Es Port's Bay in Cabrera National Park), "High" pressure (i.e., Portocolom, Sóller, Magalluf) and "Very High" pressure (i.e., Pollença, Sta.Ponça, Cala d'Or) for the impacted meadows examined here.

Sediment sampling and analyses

Three sediment cores 17–45 cm long were extracted from each seagrass meadow in July 2012 (except for those at Sta. Maria, which were collected in July 2013) by inserting PVC pipes 60 cm long and 9 cm diameter by SCUBA divers. All cores were stored frozen until processing in the lab.

Sediment accumulation rates were obtained from concentration profiles of ^{210}Pb measured in one of the cores at each site sliced every 1 cm (as explained in Mazarrasa et al. 2017). However, robust sediment age estimates were obtained for 8 out of the 11 meadows examined whereas intense mixing processes precluded the establishment of sediment chronologies for the remaining 3 meadows: Sóller, Ses Illetes, and Es Pujols.

The remaining portions of the dated cores and the other additional cores per site, sliced at 2 cm intervals, were used to determine sediment density, sediment organic matter concentration (OM, in %DW), and sediment organic carbon (C_{org}) content along the depth profile. Sediment density (DBD, g cm^{-3}) was estimated by dividing the dry weight of the sediment sample (g) (dried at 60°C during a minimum of 48 h) by the sample fresh volume (cm^3). OM (%DW) was estimated from loss on ignition, as the weight loss of dry sediment in the samples after combustion at 550°C during 4 h. Sediment organic carbon (C_{org} %DW) was measured in every other slice along the depth profile from one core per site on an Elemental Analyser - Isotope Ratio Mass Spectrometry (EA-IRMS) at Iso-Analytical Laboratory (United Kingdom) and estimated in the rest of the samples applying the relationship between OM (%DW) and C_{org} (%DW) contents measured in the same sample ($n = 101$),

$$C_{org} = -0.601\ (\pm\ 0.09) + 0.290\ (\pm\ 0.009)\ \text{OM}\ \left(F_{100=}973.8, R^2=0.91,\ p\ <\ 0.001\right)$$

obtained by Mazarrasa et al. 2017.

Bulk organic carbon (g C cm^{-3}) was estimated as the product of C_{org} (%DW) and the sediment dry bulk density (DBD) divided by 100.

Carbon sources were estimated based on the quantification of the $\delta^{13}C_{org}$. The sediment $\delta^{13}C_{org}$ signature was measured in every other slice along the depth profile from one of the cores collected per site (Table 1) using the Elemental Analyser - Isotope Ratio Mass Spectrometry (EA-IRMS) at the Iso-Analytical Laboratory (United Kingdom). We consider two main sources of C_{org} to the sedimentary stocks: seagrass tissue and sestonic matter (which includes living and non-living matter in the water column, such as microalgae and/or terrestrial detritus). The contribution of these sources to the total stock was estimated applying a two-component isotope-mixing model (Eq. 1) as described by Phillips and Gregg (2003)

$$\delta_{13}C_{sediment} = \delta_{13}C_{seagrass}\ f + \delta_{13}C_{seston}\ (1 - f) \quad (1)$$

where $\delta^{13}C_{seagrass}$ ($\pm$ SE) values correspond to averages of the $\delta^{13}C_{org}$ measured in leaves and rhizomes of *P. oceanica* shoots collected at each site in 2008 and 2009 (except for Es Port and Porto Colom, where only the leaf $\delta^{13}C_{org}$ was available and the SE considered was the average of the SEs of the other meadows $\delta^{13}C_{seagrass}$ signature). The $\delta^{13}C_{seston}$ values correspond to the values reported for the same meadows by Papadimitriou et al. (2005) except for Cala d'Or, Porto Colom and Sóller, where the average $\delta^{13}C_{seston}$ reported in Papadimitriou et al. (2005) was used (-22.1 ± 1.7) (Supporting Information Table SI 1).

In assessing the contribution of different C_{org} sources along time we also considered the potential variability in the $\delta^{13}C_{org}$ source signatures over time due to the Suess effect, i.e., the decrease in the atmospheric CO_2 and oceanic DIC $\delta^{13}C$ signature toward present derived from the burning of fossil fuels (Keeling 1979). We did so by estimating past *P. oceanica* and seston $\delta^{13}C_{org}$ signatures based on three different rates of oceanic DIC $\delta^{13}C$ depletion with time. The rates applied correspond to the slopes of the linear regression equations resultant from fitting predicted $\delta^{13}C_{org}$ increment values ($\Delta\ \delta^{13}C_{org}$) for different years within three different

Table 1. Maximum sediment core depths analyzed for $^{13}\delta C_{org}$ and C : N and the deepest layer dated by ^{210}Pb and the corresponding age.

Station	Max. depth for $^{13}\delta C_{org}$ (cm)	Max. depth for C : N (cm)	^{210}Pb dating: Max depth (cm)	^{210}Pb dating: Corresponding year
Pollença	37	35	21	1844 ± 6
Sta. Ponça	29	29	21	1887 ± 12
Cala d'Or	29	29	21	1930 ± 1
Portocolom	25	25	25	1924 ± 6
Sóller	33	33	—	—
Magalluf	41	41	17	1871 ± 8
Es Port	25	25	21	1868 ± 9
Es Pujols	25	17	—	—
Ses Illetes	21	21	—	—
Es Castell	33	33	17	1921 ± 9
Sta. Maria	33	31	17	1852 ± 8

periods (1850–1900, 1900–1950, and 1950–2010) using the equation described by Schelske and Hodell (1995) and corrected by Verburg (2007), suitable for periods between 1840 and 2000

$$\Delta\delta^{13}C_{org} = (4577.8 - 7.343 * Y) + \left(3.9213 * 10^{-3} * Y^2\right) - \left(6.9812 * 10^{-7} * Y^3\right) \quad (2)$$

where Y is the year. The rates obtained (−0.0015‰ y-1 for the period 1850–1900, −0.0073‰ y-1 for the period 1900–1950 and −0.0259‰ y-1 for the period 1950–2010, Supporting Information Fig. SI 1) were used for adjusting the $\delta^{13}C_{org}$ signature of the sources used in Eq. 1 according to the age assigned at each sediment layer.

As sources $\delta^{13}C_{org}$ may have changed along time due to variability in different environmental factors, including the Suess effect, we also measured sediment C : N ratios to further support trends in the contribution of different sources identified based on the isotopic signature, as marine algae usually have lower C : N values (C : N < 10) compared to seagrass (Meyers 1994). C : N ratios were calculated only considering the organic fraction of sediment carbon (C_{org}). N was determined for every slice of one core per site using a CN elemental analyser (Truspec CN determinator, LECO). Estimates of $\delta^{13}C_{org}$ and C : N were obtained down to the maximum sediment depth sampled, but they could only be associated to a specific date down to the oldest ^{210}Pb-derived age for each meadow (Table 1).

In those meadows where robust dates could be assigned to specific sediment layers, the burial rates of C_{org} derived from *P. oceanica* and seston were estimated using the calculated contribution of each source (%) at each sediment layer and the total C_{org} stock of the corresponding sediment layer

Table 2. Results of the linear regression analyses between δ^{13}C signature and C : N ratio with depth along the sediment profile.

	δ_{13}C					C : N				
Station	Slope	R^2	*p*-value	df	*F* ratio	Slope	R^2	*p*-value	df	*F* ratio
Pollença	0.01 ± 0.01	0.09	>0.05	10	0.86	0.12 ± 0.04	0.41	0.006	16	10.24
Sta.Ponça	−0.03 ± 0.04	0.1	>0.05	8	0.8	0.20 ± 0.09	0.26	0.049	14	4.68
Cala d'Or	0.031 ± 0.015	0.42	>0.05	7	4.42	−0.04 ± 0.07	0.032	>0.05	14	0.44
Portocolom	−0.04 ± 0.02	0.32	>0.05	6	2.4	0.27 ± 0.09	0.47	0.0095	12	9.83
Sóller	0.019 ± 0.04	0.032	>0.05	8	0.23	−0.06 ± 0.11	0.02	>0.05	16	0.28
Magalluf	0.25 ± 0.04	0.76	<0.0001	12	35.3	0.29 ± 0.04	0.73	<0.0001	20	50.32
Es Port	0.02 ± 0.02	0.1	>0.05	7	0.67	0.55 ± 0.66	0.06	>0.05	12	0.68
Es Pujols	0.39 ± 0.09	0.78	0.008	6	18.1	−0.67 ± 0.55	0.17	>0.05	8	1.48
Ses Illetes	0.04 ± 0.04	0.2	>0.05	5	0.98	−0.85 ± 1.30	0.05	>0.05	9	0.43
Es Castell	0.07 ± 0.03	0.41	0.04	9	5.65	−0.15 ± 0.19	0.04	>0.05	16	0.63
Sta. Maria	0.065 ± 0.017	0.62	0.004	10	14.6	0.076 ± 0.099	0.04	>0.05	15	0.57

divided by the time (i.e., the total accumulation period) encompassed by the segment. C_{org} stock (g C cm^{-2}) was estimated as the product of C_{org} bulk concentration and the sediment slice thickness (2 cm). To estimate the average change in the burial rates of C_{org} derived from *P. oceanica* and seston, both burial rates along time for each meadow were standardized by the burial rate measured in the year closest to 1930, the oldest date encompassed by the sediments sampled in all the meadows examined (Table 2).

Statistical analyses

A paired *t*-test was applied to assess the difference on the average $\delta^{13}C_{org}$ signature of the sediments and seagrass tissues across the meadows examined and to compare the contributions of *P. oceanica* and seston along all the sediments. Analysis of Variance (ANOVA) was used to assess the differences among meadows in sediment $\delta^{13}C_{org}$, C : N and the relative contribution (%) and bulk concentration (mg C_{org} cm^{-3}) of the carbon derived from *P. oceanica* and seston to the sediment C_{org} stock. The Tukey–Kramer HSD test was used to identify the meadows that differed significantly in the properties examined. Linear regression analysis was used to describe the rate of change in $\delta^{13}C_{org}$ and C : N with sediment depth and Ln transformed burial rates with time.

We propagated the standard error (SE) for the average $\delta^{13}C_{seagrass}$ signature across the meadows examined, the average contribution of each source per meadow and the estimated burial rates over time (Supporting Information).

Results

Sediment $\delta^{13}C_{org}$ was either uniform across the sediment profile or significantly increased (linear regression analysis, $p < 0.05$) with sediment depth in the meadows sampled at Es Castell, Es Pujols, Magalluf, and Santa Maria with mean (± SE) rates of increase of 0.07 ± 0.03‰ cm^{-1}, 0.39 ± 0.09‰ cm^{-1}, 0.25 ± 0.04‰ cm^{-1} and 0.06 ± 0.02‰ cm^{-1}, respectively (Fig. 2; Table 2). The sediment C : N ratios increased significantly (linear regression analysis, $p < 0.05$) with sediment depth in Magalluf, Pollença, Portocolom, and Santa Ponça at mean rates of 0.29 ± 0.04 cm^{-1}, 0.12 ± 0.04 cm^{-1}, 0.27 ± 0.09 cm^{-1}, and 0.20 ± 0.09 cm^{-1}, respectively (Fig. 2; Table 2).

The average sediment $\delta^{13}C_{org}$ and C : N ratio in the meadows examined varied within the range determined by the average $\delta^{13}C_{org}$ signatures and C : N ratios of the sources considered, *P. oceanica* and seston, except for Ses Illetes, where the sediment C : N ratio exceeded that of *P. oceanica* tissue (Fig. 3). The average $\delta^{13}C_{org}$ of sediment differed significantly among the meadows examined (ANOVA, $p < 0.001$, $F_{98} = 3.35$), ranging from a maximum of −15.05 ± 0.12‰ and −15.08 ± 0.21‰ in Pollença and Porto Colom, respectively, to a minimum of −18.21 ± 0.99‰ in Magalluf (Fig. 3). The average $\delta^{13}C_{org}$ of sediment was significantly lower than that for seagrass tissues in all meadows examined (paired *t*-test, $p < 0.0001$, $t = -6.53$, df = 10), confirming the contribution of an isotopic lighter carbon source, such as seston (average $\delta^{13}C_{org} = -21.65 \pm 0.34$‰). The C : N ratio also differed significantly across sites (ANOVA, $p < 0.0001$, $F_{162} = 21.28$), ranging from a maximum of 53.6 ± 2.8 in Ses Illetes to a minimum of 10.5 ± 0.6 in Cala d'Or (Fig. 3).

The two-component isotope mixing model revealed that *P. oceanica* had a significantly greater contribution to the total C_{org} stock (59% ± 12%) than seston (41% ± 8%) across all sediments examined (paired *t*-test, $p < 0.001$, $t = -3.49$, df = 98). However, the average contributions of each source differed significantly across meadows (ANOVA, $p < 0.0001$, $F_{98} = 9.91$; Tuckey–Kramer HSD, α = 0.05; Fig. 4) with Ses Illetes and Santa Maria showing the highest contribution of *P. oceanica* (86% ± 13% and 81% ± 10%, respectively) and Es

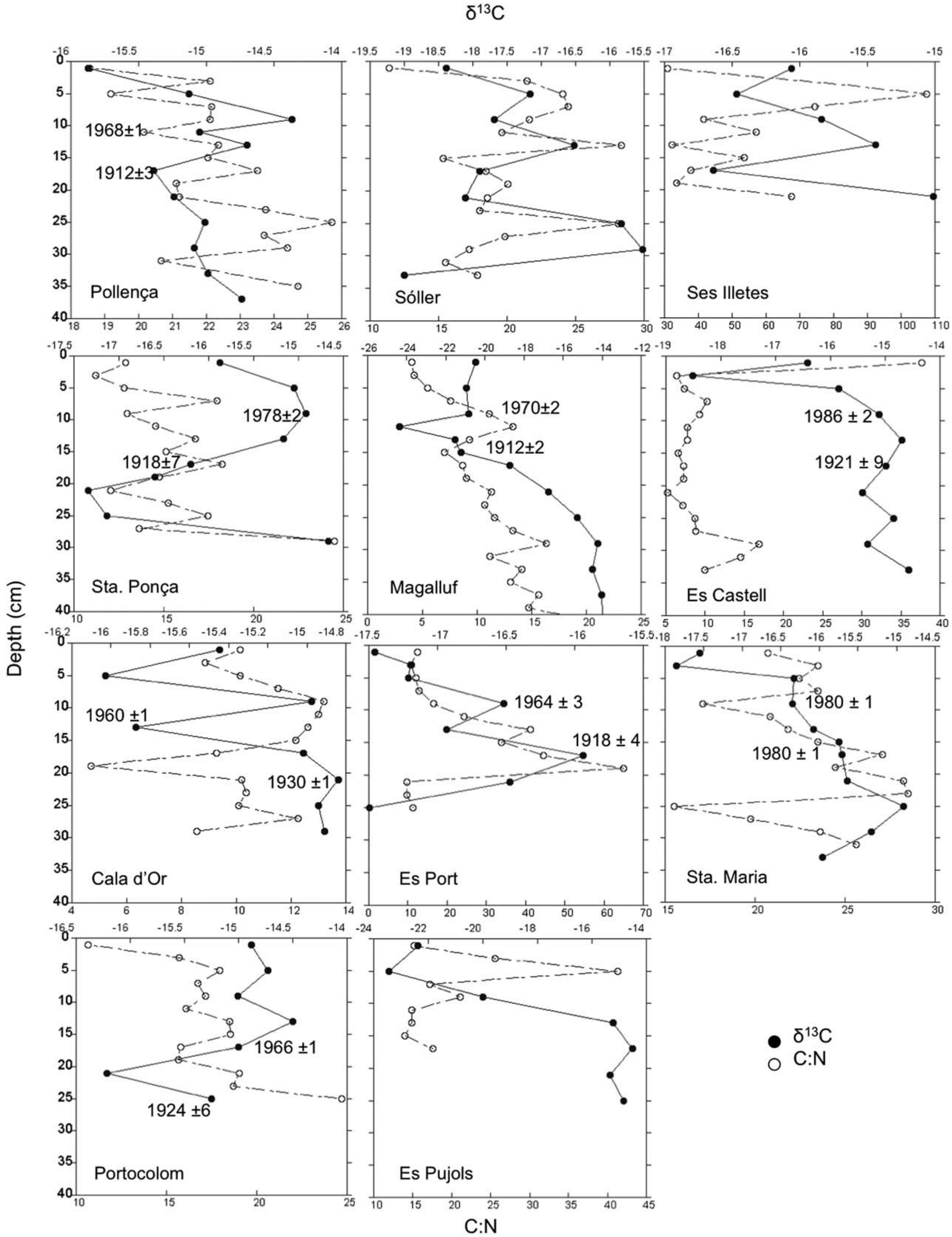

Fig. 2. $\delta^{13}C_{org}$ and C : N along sediment depth profiles at each station. Dates derived from the ^{210}Pb age models are shown in those meadows where the sediments could be dated. Panels are ordered from "very high" to "low" human pressure from up to down and from the left to the right.

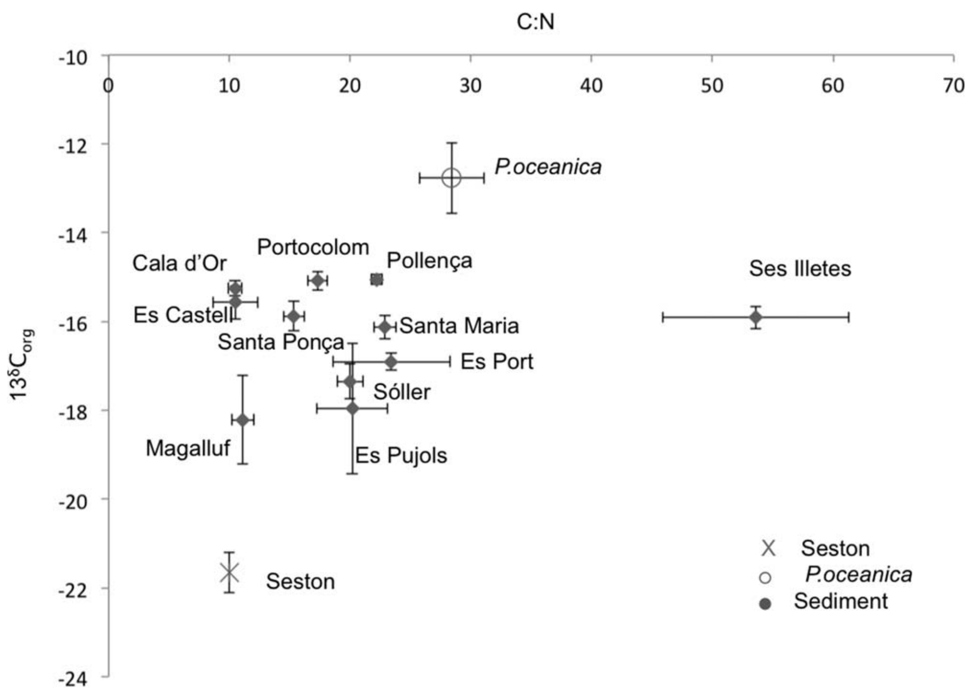

Fig. 3. Cross plot of C : N elemental ratios and $\delta^{13}C_{org}$ of the sources considered in this study (*P. oceania* and seston) and the average values measured along the sediment profile in each meadow. C : N values for *P. oceanica* and seston were taken from Fourqurean et al. (2007) and Meyrs et al. (1994), respectively.

Port and Magalluf showing the lowest contribution of *P. oceanica* (19.6% ± 4.3% and 33.2% ± 9.4%, respectively) and the highest contribution of seston (80% ± 11% and 67% ± 10%, respectively). The contribution of *P. oceanica* was, on average, significantly higher (80% ± 9%) in the pristine meadows (i.e., under low human pressure) than in impacted ones (i.e., from moderate to very high human pressure) (52% ± 12%) (ANOVA, $F_{98} = 26.65$, $p < 0.0001$), whereas the average contribution of seston in the impacted meadows was significantly higher (48% ± 11%) than that in the most pristine ones (20% ± 3%) (ANOVA, $F_{98} = 26.65$, $p < 0.0001$) (Supporting Information Fig. SI 2a). Similarly, the meadows examined showed significant differences in the C_{org} bulk concentration derived from each source (Supporting Information Table SI 2) and whereas there were no significant differences in terms of *P. oceanica* derived C_{org} between the impacted meadows (7.7 ± 2.0 g C_{org} cm^{-3}) and the most pristine ones (8.0 ± 2.1 g C_{org} cm^{-3}) (ANOVA, $F_{94} = 0.05$, $p > 0.05$), the average bulk concentration of C_{org} derived from seston was significantly higher in meadows exposed to moderate to very high human pressure (6.2 ± 1.6 g C_{org} cm^{-3}) compared to that in meadows under low human pressure (1.6 ± 0.4 g C_{org} cm^{-3}) (ANOVA, $F_{94} = 0.05$, $p < 0.0001$) (Supporting Information Fig. SI 2b).

The contribution of *P. oceanica* and seston to the sediment C_{org} stock changed over time, showing, in general, a decrease in the contribution of *P. oceanica* and an increase in the sestonic carbon toward present (Fig. 5). For those meadows where seston $\delta^{13}C_{org}$ was not available (Cala d'Or and Porto Colom) and the regional average (± SE) was used, the propagated SEs were very large and precluded the identification of clear trends. The observed trends change when the isotopic mixed model is corrected by considering the Suess effect on the $\delta^{13}C_{org}$ signature of the sources (Supporting Information Fig. SI 3).

Examination of the average burial rate of each carbon source along time across all the meadows showed that the burial rate of C_{org} derived from seston (2.8 ± 0.6% y^{-1}; $p < 0.0001$, $R^2 = 0.38$, $F_{38} = 22.45$) increased at a higher rate than that of *P. oceanica* derived C_{org} (2.3 ± 0.6% y^{-1}; $p < 0.0001$, $R^2 = 0.47$, $F_{33} = 29.53$) (Fig. 6), with similar trends observed in most of the individual meadows examined (Supporting Information Fig. SI 4).

Discussion

The average sediment $\delta^{13}C_{org}$ and C : N values in the meadows examined fall between the $\delta^{13}C_{org}$ and C : N values characteristic of seston previously measured in the study sites ($\delta^{13}C_{org} = -21.6 \pm 0.4‰$, Papadimitriou et al. 2005) and reported in the literature (C : N ratio < 10, Meyers 1994) and those of *P. oceanica* carbon measured in the region ($\delta^{13}C_{org} = -12.8 \pm 0.8‰$; C : N = 28.4, Fourqurean et al. 2007). This is consistent with the assumption that the

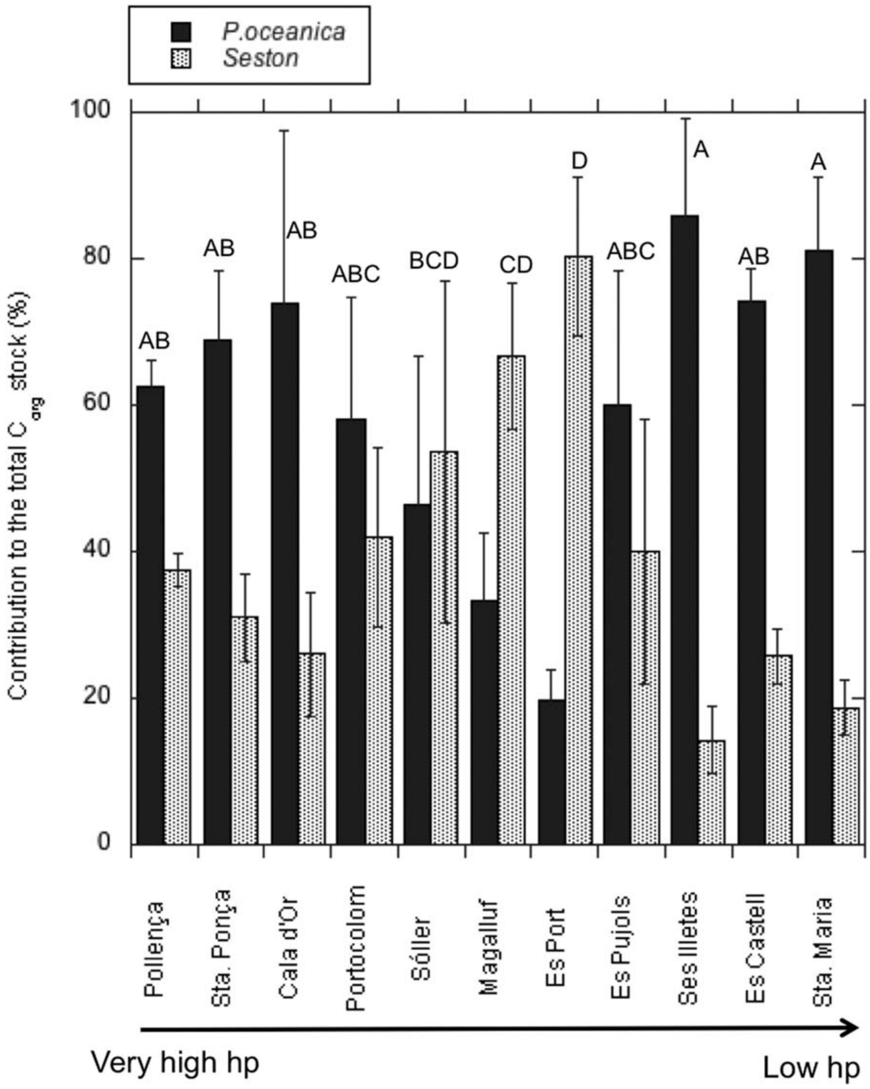

Fig. 4. Sestonic and *P. oceanica* average (± SE) contribution (%) to the total carbon stock measured in the sediment profiles. X axis is ordered from the meadows under "Low" human pressure (Low hp) toward those under "Very high" human pressure (High hp). Stations not connected by same letters are significantly different (Tukey–Kramer HSD, $\alpha = 0.05$).

sediment C_{org} pool in the seagrass sediments examined corresponded to a mixture of carbon derived from *P. oceanica* and seston. Although the sediments from Ses Illetes, in Formentera, showed a higher C : N ratio (54 ± 8), this value is still consistent with maximum C : N ratios reported for *P. oceanica* tissue (47.7, Fourqurean et al. 2007).

The two-component isotope mixing model, considering *P. oceanica* and seston as the two main potential sources of carbon, allowed estimating that 41% ± 8% of the total C_{org} sediment stock in the meadows studied has a sestonic origin whereas the remaining 59% ± 12% consists of *P. oceanica* derived carbon. This average contribution of *P. oceanica* to the total carbon stock is comparable to previous global estimates where seagrasses contribute about 50% of the C_{org} in seagrass sediments (Kennedy et al. 2010). However, the contribution of seagrass and seston to the sediment C_{org} varied greatly across meadows.

The highest contribution of *P. oceanica* to the top meter C_{org} stock (about 80%) was found in two of the meadows under "low" human pressure in this study: Ses Illetes, a non-urbanized beach in Formentera Island (Roig-Munar et al. 2013) and Santa Maria, one of the two most pristine sites of the study located in Cabrera National Park. Conversely, the highest contribution of seston (80% ± 3%) to the sediment C_{org} stock was found in the meadow at Es Port, also in Cabrera National Park, followed by that at Magalluf (67% ± 10%) under relatively "moderate" and "high" levels of human pressure, respectively. Es Port concentrates most of the

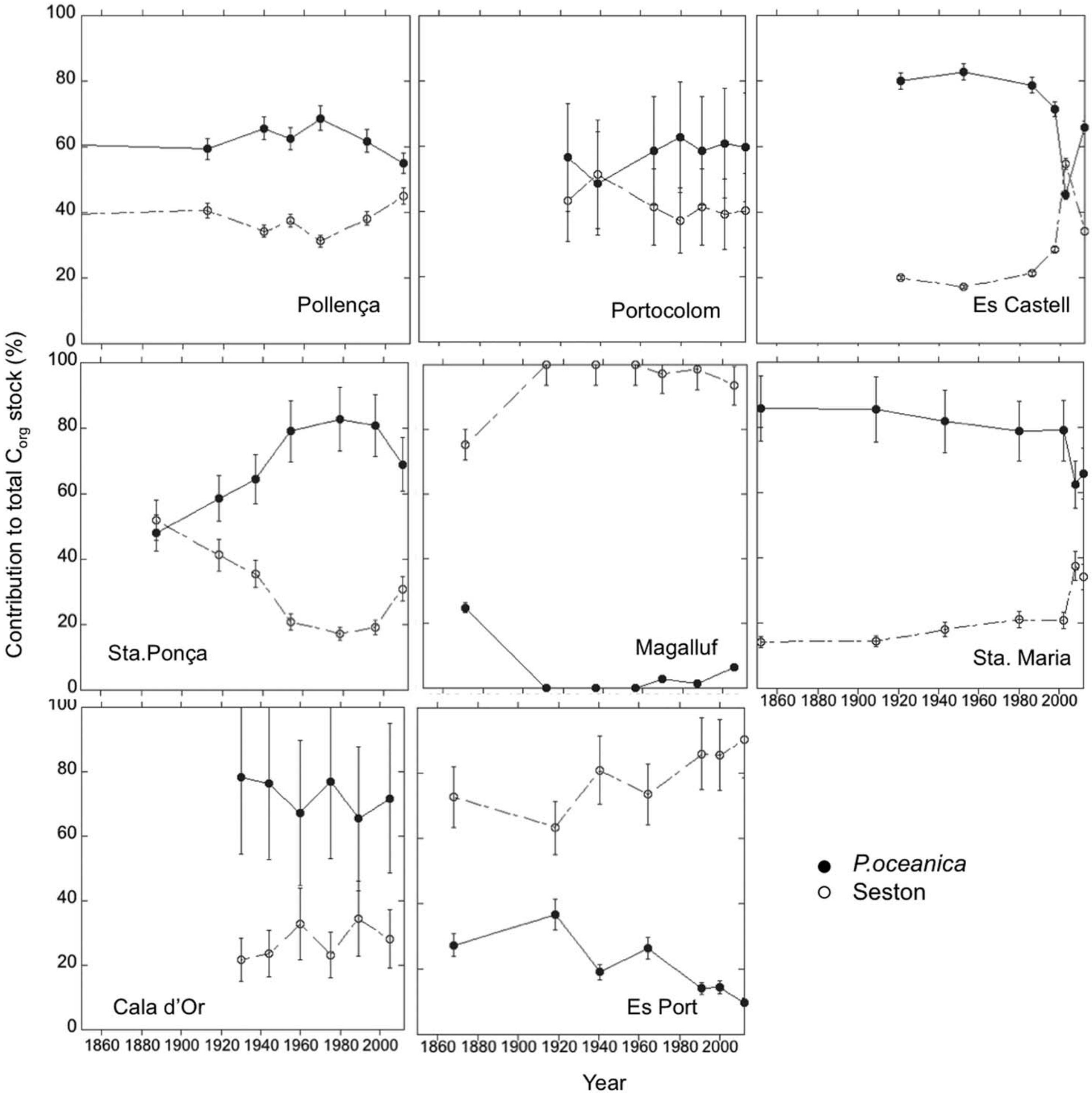

Fig. 5. Estimated contribution (± SE) of *P. oceanica* and seston to the carbon pool with time at each station for those meadows where the sediment could be dated. Panels are ordered from "very high" to "low" human pressure from up to down and from the left to the right.

human pressure within the Cabrera Archipelago, receiving the sewage produced by visitors in moored ships, usually discharged raw into the water, as well as the treated sewage produced by the visitors on land (Marbà et al. 2002; PNMTAC 2009). In addition, Es Port is a very sheltered bay with a relatively long water residence time (11 d) that enhances the sinking of particles from the water column (Marbà et al. 2002; Holmer et al. 2004), likely leading to the largest contribution of allochthonous carbon to the sediment stock compared to other meadows under higher

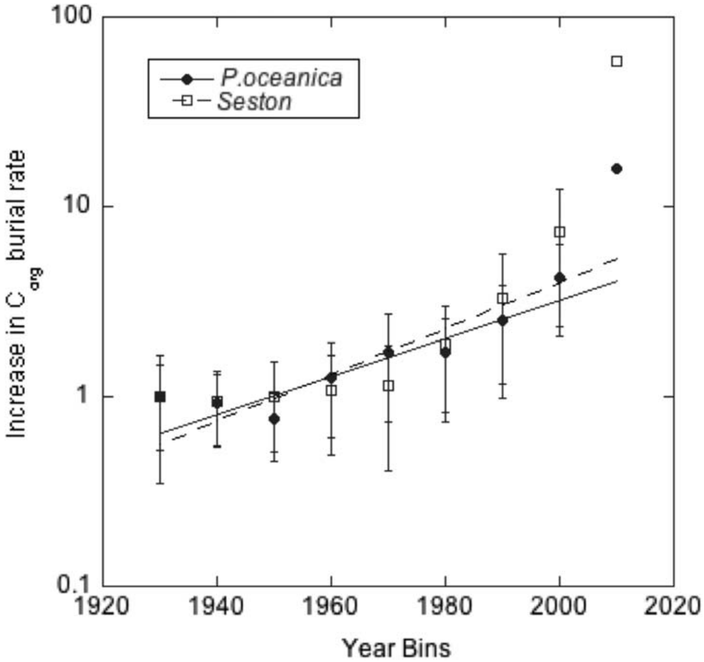

Fig. 6. Change in burial rates of *P. oceanica* and seston derived-C_{org} since 1930 in the seagrass meadows examined. The values represented are averages ($\pm$ SE) of C_{org} burial rates along the sediment profile standardized by the C_{org} burial rate estimated for the year $\sim$ 1930 (the most ancient layer in common for all the meadows examined), grouped by 10 yr bins. Solid and dashed lines show the fitted linear regression equations $\ln(y) = -0.44 + 0.023$ ($\pm$ 0.006)*x ($R^2 = 0.47$, $p < 0.0001$) and $\ln(y) = -0.57 + 0.028$ ($\pm$ 0.006)*x ($R^2 = 0.37$, $p < 0.0001$) obtained by plotting standardized burial rates for *P. oceanica* and seston derived C_{org} respectively, against time (years).

human pressure. The contribution of seston (26–54%) and *P. oceanica* (75–45%) to carbon sediment stocks was more similar among the rest of the meadows, all of them supporting a moderate to very high level of human pressure, except for Es Castell (in Cabrera National Park), which is classified under "Low" human pressure. Yet, Es Castell, located at the sheltered entrance of Es Port Bay, is exposed to eutrophied waters from the port of Cabrera, which might explain the slightly larger contribution of seston (26% ± 4%) to the C_{org} sediment stock relative to that found in Sta. Maria (19% ± 4%), the other pristine site of the park.

These results suggest that, despite seagrass-derived organic carbon tended to be the dominant contributor to the total C_{org} sediment stock, the composition of the sediment C_{org} stocks in the meadows examined differed in terms of the sources (i.e., *P. oceanica* vs. seston), which could be explained by the different level of human pressure supported. The sediment carbon deposits in the most pristine meadows showed, on average, a significantly greater contribution of carbon derived from *P. oceanica* and a significantly lower contribution of sestonic derived carbon compared to impacted meadows (those under moderate to very high human pressure) (Supporting Information Fig. SI 2a). This trend was clearer when considering the average C_{org} bulk concentration derived from each source, especially in the case of seston-derived C_{org}, which was significantly lower in the most pristine sites (e.g., Es Castell, Sta. Maria, and Ses Illetes) compared to that in the meadows supporting "moderate" to "very high" human pressure (Supporting Information Table SI 2; Supporting Information Fig. SI 2b). Yet, other factors such as the configuration of coastal areas likely plays a significant role by favoring the accumulation of allochthonous carbon available in the water column in sheltered meadows (Marbà et al. 2002; Van Keulen and Borowitzka 2003).

The results also show a general temporal variability in the contribution of the different carbon sources to the sediment deposits. The $\delta^{13}C_{org}$ signature tended to decrease toward the sediment surface, pointing to a shift in the relative contribution of the sources. Indeed, the results of the two-component isotope mixing model in the dated sediments showed that the contribution of *P. oceanica* decreased over the past 30–50 yr, whereas the contribution of sestonic carbon tended to increase in most of the meadows examined. The decrease in the C : N ratio toward the surface in four of the meadows examined also suggests an increase in seston, characterized by a lower C : N ratio (C : N < 10; Meyers 1994) compared to seagrass.

However, the results of the mixing model applied assuming constant $\delta^{13}C_{org}$ for the sources, need to be considered with care. The Suess effect tends to attenuate the trends outlined above on the results of the mixing model, although the decreasing rates in the DIC $\delta^{13}C$ signature with time used might be overestimated due to the model applied for their estimation, as explained by Verburg (2007). In addition, other environmental factors and processes could have affected the $\delta^{13}C$ signature of the C_{org} sources over time, hindering the interpretation of these results.

The increase in DIC since Industrial Revolution due to the rise in atmospheric CO_2 (Friedli et al. 1986) is expected to have enhanced the isotopic discrimination in marine plants resulting in a decrease in their $\delta^{13}C_{org}$ signature, especially for those groups known to be CO_2 limited, such as seagrasses (Durako and Sackett 1993; Zimmerman et al. 1997), compared to macroalgae or phytoplankton communities (Falkowski 1994; Beer and Koch 1996). A depletion in the $\delta^{13}C_{org}$ of seagrasses in response to higher DIC concentration has been demonstrated experimentally (Durako and Sackett 1993) and in situ observations demonstrated a spatial variability in the $\delta^{13}C_{org}$ of phytoplanktonic communities consistent with different ambient CO_2 concentrations (Rau et al. 1989; Rau 1994). However, both the increase in DIC and the Suess effect would provide a similar signal at a regional scale, resulting in a similar trend of decreasing $\delta^{13}C_{org}$ toward the surface of the sediments. Hence, a dominant role of any or both of these effects is inconsistent with the variable patterns of $\delta^{13}C_{org}$ with sediment depth and age observed among the meadows examined here.

Temperature can also control the carbon isotopic ratio in primary producers by controlling the CO_2 solubility in the water column (Rau et al. 1989; Hemminga and Mateo 1996). Warming of the Mediterranean Sea during the past century (Béthoux 1990; Romano and Lugrezi 2007), particularly intense over the last 3–4 decades (Lejeusne et al. 2010), could have decreased the CO_2 solubility, resulting in a higher likelihood of CO_2 limitation and lower discrimination for primary producers, leading to an enrichment in the $\delta^{13}C_{org}$ of the sediment toward present. Moreover, photosynthetic rates are expected to increase with warming (Harris et al. 2006), which would result in enhanced CO_2 limitation and reduced carbon isotopic discrimination. However, the trend expected from warming is opposite to the $\delta^{13}C_{org}$ decreasing trend toward present found in the sediments of some of the meadows examined. In addition, warming, like the Suess effect and the increase in DIC, operates at the regional scale, and thus may contribute to temporal variability in the sediment $\delta^{13}C_{org}$ in the meadows examined but can not explain differences in the trends observed across them.

Light availability also modulates the isotopic discrimination in primary producers by controlling the photosynthetic CO_2 demand (Lepoint et al. 2003; Vizzini and Mazzola 2003; Mateo et al. 2010). Whereas long-term records in the Balearic Islands are not available, water transparency, which depends on the concentration of suspended particles, nutrients supply and subsequent eutrophication process (Short and Burdick 1996), is likely to have decreased during the last century driven by the increase in human pressure and urbanization in coastal areas (Bowen and Valiela 2001; Duarte 2002; Lee et al. 2006). Indeed, the Mediterranean Sea is undergoing a process of eutrophication for at least the last 3–4 decades (Mateo et al. 2010), with an intensity likely variable among sites depending on the level of anthropogenic pressure. Eutrophication may lead to a reduction in seagrass photosynthetic rates and to an increase in isotopic discrimination but also to an increase in the load of phytoplankton and seston, expected to lead to an increase in sedimentation rates of these materials in the underlying seagrass sediments.

Finally, even if the contribution of the various sources had been constant over time, a decrease in $\delta^{13}C_{org}$ toward the sediment surface could result from the higher burial efficiency of the seagrass C_{org} compared to that of seston. However, higher remineralization of seston compared to seagrass carbon, which would lead to an increase in $\delta^{13}C_{org}$ with depth, should be accompanied by a decline in the concentration of organic matter with depth (Garten et al. 2007). Such a decline in organic matter along with an increase in $\delta^{13}C_{org}$ with depth was only observed in the meadow at Es Pujols (Mazarrasa et al. 2017) suggesting that a different degree of remineralization of the sources cannot account for the patterns observed in $\delta^{13}C_{org}$ with depth in most of the meadows of this study. In addition, the effect of diagenesis may also be discarded as sediment organic matter, including seagrass tissues, seem to experience, in general, non or little change in the $\delta^{13}C_{org}$ signature due to decomposition (Zieman et al. 1984; Meyers 1994; Mateo et al. 2001; Fourqurean and Schrlau 2003).

Hence, we conclude that the most reasonable explanation for the decrease in $\delta^{13}C_{org}$ of the sediment carbon stock toward present observed in some of the meadows examined is the increase in the input of allochthonous carbon, derived from eutrophication and enhanced particle sedimentation resulting from urbanization and increase in the usage of coastal areas in the study region since the 60's. This hypothesis is supported by the exponential increase in the burial rate of seston-derived C_{org} for the last century in the meadows examined, which is faster than that found for *P. oceanica*-derived C_{org}, especially since the 60's decade (Figure 6). These results are consistent with what has been found in other regions of the world, such as Botany Bay, in Sydney (Australia; Macreadie et al. 2012), Oyster Harbour (SW Australia; Serrano et al. 2016), or Southern Chile (Mayr et al. 2014), suggesting that the shift toward more sestonic enriched carbon deposits in seagrass sediments might be a global phenomenon in areas under a significant recent increase in anthropogenic pressure.

In summary, the contribution of *P. oceanica* and seston to the carbon deposits in the sediments examined varied spatially and temporally due to local differences in anthropogenic pressure and its rise during the last century. Inputs of carbon from both sources have, on average, increased in recent decades. However, the burial of seston derived C_{org} has increased faster than that of seagrass, consistent with a likely general eutrophication associated with the intensification of the anthropogenic pressure in the coasts of the region of study. The general enrichment in sestonic carbon identified toward present might imply the weakening of the carbon deposits (Macreadie et al. 2012), as they become more labile and easier to remineralize, and therefore more vulnerable to disturbances.

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Acknowledgments

We thank the support of the Generalitat de Catalunya to MERS (2014 SGR – 1356). We thank Regino Martínez and Fernando Lázaro for field work support and Laura Oliver for laboratory assistance. We thank the ferry company Baleària for supporting travel between islands. This study was funded by the EU FP7 project Operas (contract number 308393) and the project EstresX funded by the Spanish Ministry of Economy and Competitiveness (contract number CTM2012-32603). I.M. was supported by a Ph.D. scholarship of the Government of the Balearic Islands. AAO was supported by a Ph.D. grant of Obra Social "la Caixa." This work is contributing to the ICTA 'Unit of Excellence' (MinECo, MDM2015-0552).

Conflict of Interest

None declared.

Submitted 25 November 2015
Revised 19 May 2016; 03 November 2016
Accepted 05 December 2016

Associate editor: Josette Garnier