Contribution of Posidonia oceanica meadows in the context of climate change mitigation in the Mediterranean Sea

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Abstract

Coastal marine vegetation has been recently highlighted for its highly efficient carbon storage capacity. Among the sixty-four species of seagrass, *Posidonia oceanica*, a Mediterranean endemic species, appears to be the most effective in carbon fixation and storage. Based on new data from the study of one of the largest *P. oceanica* meadows in the Mediterranean Sea (100 km of coastline, 20 425 ha), and a synthesis of available data from the whole of the Mediterranean basin, the aim of this work is to evaluate the amount of carbon fixed each year by *P. oceanica* and sequestered in the matte, in relation with the mitigation of the impact of climate change (carbon sink).

The mean total carbon fixation (blades, sheaths and rhizomes) per year varies between 33.5 and 426.6 g $C.m^{-2}$ and the mean carbon sequestration (long-term sink in the matte), corresponding to the sheath and rhizome tissues, varies between 7.7 and 84.4 g $C.m^{-2}$, with a clear decreasing trend according to depth because of the meadow density decrease.

The synthesis of a hundred measurements made throughout the Mediterranean Sea and at depths between 0.5 and 32.0 m provides a basis for estimating the average annual carbon fixation and sequestration rate throughout the Mediterranean basin. The fixation of the blades is estimated at 1 024 t $C.ha^{-1}.yr^{-1}$, that of the sheaths at 220 t C $ha^{-1}.yr^{-1}$ and that of the rhizomes at 58 t C $ha^{-1}.yr^{-1}$; *i.e.* a total fixation rate of 1 302 t C $ha^{-1}.yr^{-1}$ and sequestration rate (dead sheaths and rhizomes) of 278 t C $ha^{-1}.yr^{-1}$. This annual carbon fixation represents only 0.61% on average of CO_2 emissions/releases for all Mediterranean countries but in the large Mediterranean islands this fixation is on average 3.1% and can reach almost 14.4% for Corsica. Moreover, the major advantage of the *P. oceanica* meadow lies in its capacity to store carbon from annual carbon sequestration for centuries to millennia and can be compared to several terrestrial ecosystems considered to be efficient in carbon storage (peatlands).

Key words: Seagrass; *Posidonia oceanica;* Carbon Fixation; Carbon Sequestration; Mediterranean Sea; Corsica.

Introduction

At the 21st meeting of the Conference of the Parties (COP 21) of the Climate Change Convention, all participants adopted the Paris Agreement. This agreement stipulates in Article 5 that '*Parties should take action to conserve and enhance, as appropriate, sinks and reservoirs of greenhouse gases'* (FCCC, 2015). On the other hand, while previous conferences had focused on forest-based sinks (Kyoto Protocol), for the first time COP 21 noted '*the*

importance of ensuring the integrity of all ecosystems, including oceans'. Major carbon sinks such as wetlands, peatlands, coastal vegetation and phytoplankton were, therefore, for the first time taken into account.

The concept of carbon sink covers several very different compartments, which are often erroneously confused in the literature. (i) Long-term sinks correspond to carbon which is not re-mineralized after the death of the primary producer and therefore sequestrated for thousand or million years. This sink corresponds to coal, peat and modern deposits. (ii) Short-term sinks correspond to the amount of carbon which is incorporated into living matter, for a few days to millennia, depending upon the life span of the organisms: days for phytoplankton, months for leaves, centuries to millennia for tree trunks. In fact, this corresponds to the biomass. Part of the so-called carbon sequestration by the European forests is just due the expansion of forests, following agricultural decline, and to the ageing of forests, which accumulate carbon in the wood; this carbon is more or less slowly mineralized after the death of the leaves or of the whole plant. (iii) A number of plants and habitats, such as *Posidonia oceanica* (Linnaeus) Delile (see below), may fall in between, due to the very low rate of re-mineralization of some tissues (rhizomes and roots), accumulated in the soil, able to persist during several millennia.

Despite a very small surface area (less than 0.5% of the oceans), coastal vegetation plays a major role in the fixation and sequestration of Blue Carbon (Nellemann *et al*., 2009; Fourqurean *et al*., 2012). In fact, these ecosystems, such as seagrass beds, kelp forests, mangroves, salt marshes and wetlands, are major carbon sinks (Chmura *et al*., 2003; Duarte *et al.,* 2005; Bouillon *et al.,* 2008; Reed & Brzezinski, 2009).

Carbon sequestration by seagrass is estimated at 15% of the blue carbon while covering only 17.7 to 61.0 million hectares at the biosphere scale (Duarte & Chiscano, 1999; Spalding *et al*., 2003; Kennedy & Björk, 2009 ; UNEP-WCMC, 2018). Among the sixty-four species of seagrass (Guiry & Guiry, 2020), *P. oceanica*, a Mediterranean endemic species, appears to be the most effective in carbon storage (Pergent *et al.,* 1994; Mateo *et al*., 2006; Kennedy & Björk, 2009; Pergent *et al*.,2014; Jamaludin, 2015. The *P. oceanica* meadow is the only ecosystem able to 'compete' with peatlands (IPS, 2008) and mangroves (Bouillon *et al*., 2008) because it builds a unique structure: the matte (Boudouresque *et al*., 2012). Made up of rhizomes and roots with sediment that fills the interstices, this little putrescible structure can reach several meters in height, and the organic and inorganic carbon inside can persist for millennia (Romero *et al*., 1994; Mateo *et al*., 1997; Lo Iacono *et al.*, 2008; Tomasello *et al*., 2009; Boudouresque *et al*., 2016; Monnier *et al*., *in press*).

The surface area covered by *P. oceanica* meadows in the Mediterranean Sea has been the subject of several estimates (Pasqualini *et al*., 1998, UNEP-MAP-RAC/SPA, 2009; Giakoumi *et al.*, 2013; Telesca *et al*., 2015). The scarcity of data for the eastern basin detracts from the accuracy of these estimates, although recent mapping works of Topouzelis *et al*. (2018) and Traganos *et al*. (2018), for the Greek coastline (32% of the Mediterranean coastline), Akçali *et al.* (2019) and Duman *et al*. (2019) for 3 000 km of Turkish Mediterranean coastline, have made it possible to improve the accuracy of the previous estimates.

On the other hand, the increase of the amount of data concerning primary production by *P. oceanica* at many sites including different locations, depths, meadow structure and human pressures, has made it possible to estimate a probable mean value of the amount of carbon fixed by *P. oceanica* at the scale of the Mediterranean basin (Buia *et al*., 1992; Pergent-Martini *et al*., 1994; Pergent *et al*., 1997; Torricelli & Peirano, 1997; Zupo *et al*., 1997; Guidetti *et al*., 2000; Cebrian & Duarte, 2001; Vela *et al*., 2006). Moreover, the use of lepidochronology associated with the analysis of the elementary composition of tissues allows determination of the part of this carbon sequestered within the matte mainly through rhizomes and dead sheaths (Pergent *et al*., 1994; Pergent-Martini *et al*., 1994; Cebrian & Duarte, 2001; Gobert *et al*., 2005; Vela *et al*., 2006; Scartazza *et al*., 2017).

Based on new data concerning one of the largest *P. oceanica* meadows in the Mediterranean Sea (100 km of coastline, 20 425 ha; Valette *et al*., 2019) and the synthesis of available data from the whole of the Mediterranean basin, the aim of this work is (i) to evaluate the amount of carbon fixed each year by *P. oceanica* and sequestered in the matte, and (ii) to better understand this ecosystem service in relation with the mitigation of the impact of climate change (carbon sink) for each Mediterranean country.

Material and method

The distribution of *P. oceanica* along the Corsican coast is conventionally subdivided into 14 sectors with similar environmental conditions (Meinesz *et al*., 1990; Pasqualini *et al*., 1998; Valette *et al*., 2019). The study area is located along the eastern coast of Corsica (Western Mediterranean Sea) characterized by the presence of an extensive *P. oceanica* meadow, designated as a NATURA 2000 site 'FR9402014 - Grand Herbier de la Côte Orientale' (Valette *et al*., 2019; Fig. 1). Sampling stations are located at 5, 10, 15, 20, 25 and 30 m depth and distributed from north to south.

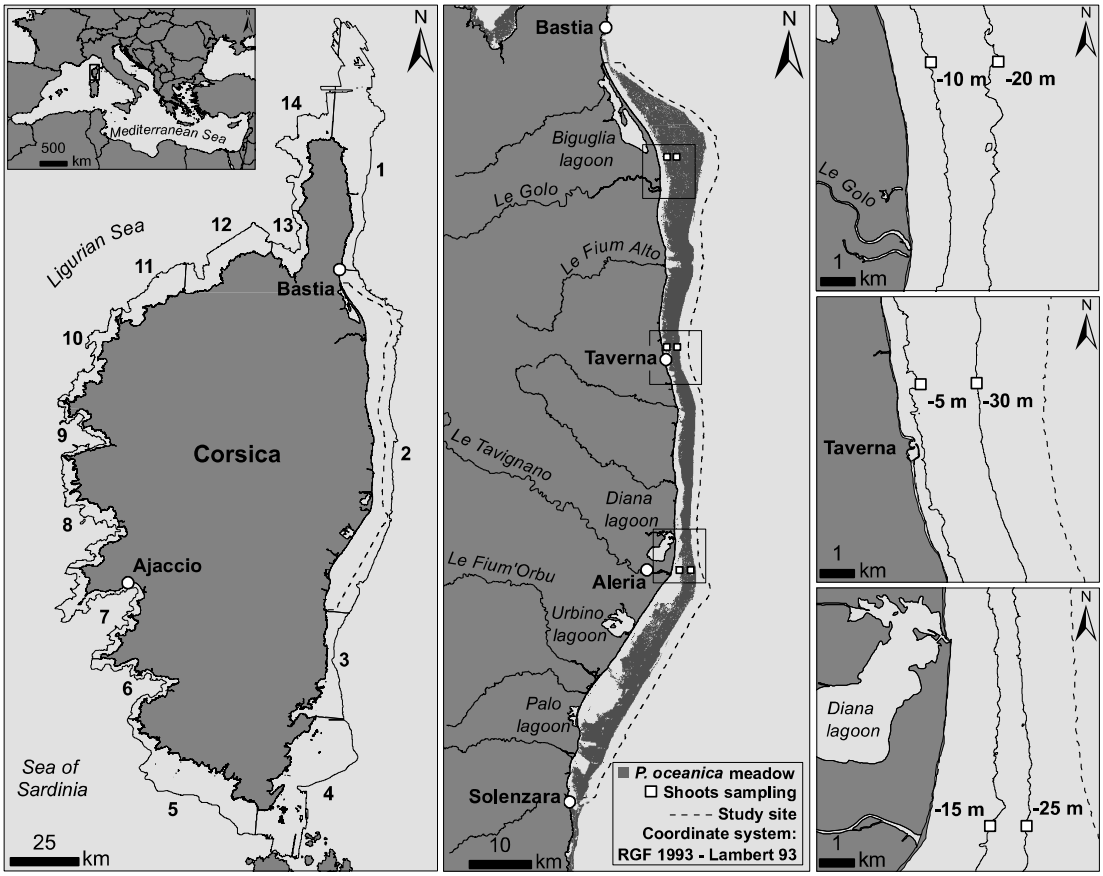

Figure 1: Left: Corsica island, with sectors 1 through 14. Middle: The studied sector (sector 2). Right: Location of the study sites and sampling stations of *P. oceanica* shoots.

The meadow density (number of shoots per square meter – shoot.m^{-2}) was measured for each station (0.16 m^2 quadrat, 20 replicates) while 20 orthotropic shoots of *P. oc*eanica were collected every three months, from July 2015 to July 2016.

A phenological analysis (Giraud, 1979), and a lepidochronological study (Pergent, 1990) were performed. The primary production was estimated according to the crossed lepidochronological method (Vela, 2006), derived from Pergent & Pergent-Martini (1990). A leaf is formed by a basal non-photosynthetic sheath and a blade. The blade primary production was estimated considering: the average number of annually produced leaves, the average length of the rank 3 adult blades (usually the longest leaf of the shoot), the average width of the rank 1 adult blades, the average density (ratio of leaf area to leaf dry mass) of the rank 1 adult blades (leaf growth completed). The sheath production was estimated considering: the average number of annually produced leaves, the average length, width and density of the rank 1 adult sheaths.

Rhizome production was assessed from the segments of the rhizome, with inserted roots, between each pair of dead sheaths of minimum thickness (corresponding to the tissue produced during a one-year period) cut and then dried for 48 h at 70 °C, until constant dry weight was achieved. Hereafter, 'rhizomes' always means 'rhizomes and roots' due to the fact than root tissues are very limited. The portions corresponding to the two most recent

years were not considered because their growth is not yet complete (Boudouresque *et al*. 1984).

The carbon content (% C) of adult blades, sheaths and rhizomes, expressed in dry mass (DM) percentage, were determined for each sample using elementary analysis (Elementar Vario MICRO Cube®, Elementar Analysensysteme GmbH, Germany).

A 95% confidence interval for each mean was computed. A Shapiro-Wilk test is applied to check the normality of the means; this is one of the most powerful normality tests (Ghasemi & Zahediasl, 2012). Student's t-test is used for comparing the means, while confidence interval (95%) is reported for non-linear regression (Minitab software™). Inter-relationships between variables were investigated by performing Pearson correlation test. The correlation coefficient was calculated together with p-values to determine the significance and strength of each relationship. A significant difference is considered as a p-value<0.05.

Results

Meadow density decreases regularly with depth, from 550.5 shoots.m^{-2} at -5 m to 106.1 shoots.m^{-2} at -30 m (Fig. 2). The number of leaves produced each year also exhibits a declining trend from shallow water to deep water (from 8.55 to 6.35 leaves.yr^{-1}; Fig. 2).

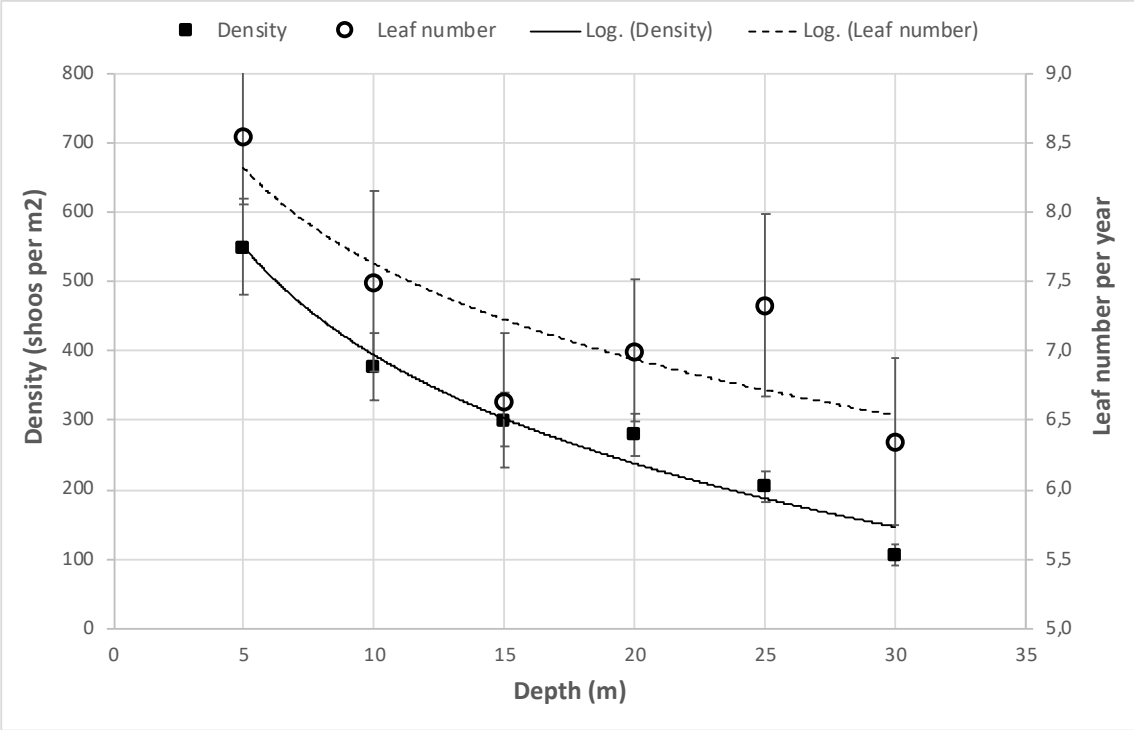

Figure 2: Meadow density (mean number of shoots.m^{-2} and confidence level) and number of leaves produced annually (mean number per shoot and confidence level) according to depth. Density trend curve: y = -226.1 x ln(depth) + 914.8 (R^2= 0.91); leaf number trend curve: y = -1.045 x ln(depth) + 10.093 (R^2 = 0.73).

Whatever the depth, the adult blade of rank 1 (external leaf) is on average shorter than the adult blade of rank 3 (t-test, p-value<0.0001) due to the higher percentage of leaves broken by herbivore grazing and water movement. The mean density of the blades of rank 1 and rank 3 is not significantly different (3.68 ± 0.44 and 3.85 ± 0.38 mg DM.cm^{-2}, respectively; t-

test, p-value=0.579). Conversely, the density of blades is always significantly smaller than sheaths (9.11 ± 1.27 mg DM.cm^{-2}; t-test, p-value<0.0001). Blade and sheath density decrease significantly with depth (respectively R^2 = 0.98, p-value<0.0001 and R^2 = 0.89, p-value<0.005; Fig. 3).

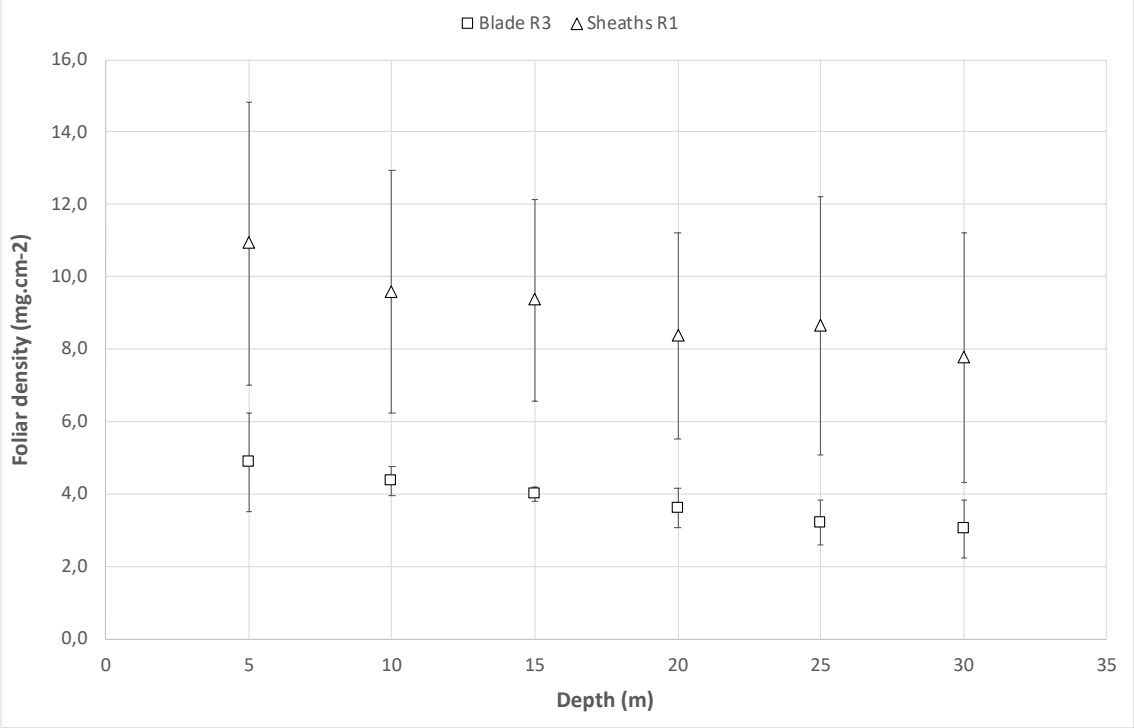

Figure 3: Blades and sheaths density (mean and confidence level 95%) according to depth. The high values of the confidence interval are related to seasonal variations in leaf tissue density.

The mean carbon content in the leaves shows no significant difference between blades (41.3 ± 0,4 %) and sheaths (41.1 ± 0.7 %) (t-test, p-value=0.663; Table I). However, the mean carbon content in rhizomes is higher (42.2 ± 0.7 %) and exhibits a significant difference with blades (t-test, p-value=0.022) and sheaths (t-test, p-value=0.024).

Table I: Carbon content (in %; mean and confidence level 95%) in *P. oceanica* leaves according to depth and sampling period (July 2015 to July 2016).

	-5 m		**-10 m**		**-15 m**	
	Blades	Sheaths	Blades	Sheaths	Blades	Sheaths
July	41.2 ± 1.9	43.0 ± 2.5	41.9 ± 1.2	43.0 ± 2.2	42.2 ± 0.6	42.6 ± 2.8
October	41.3 ± 1.1	40.2 ± 1.2	42.9 ± 0.3	41.7 ± 2.3	40.4 ± 1.1	41.0 ± 0.3
January	40.7 ± 0.2	37.7 ± 3.1	40.6 ± 0.4	38.2 ± 3.7	40.1 ± 0.2	37.6 ± 2.7
April	40.5 ± 4.2	40.0 ± 3.1	41.7 ± 2.6	40.4 ± 3.9	42.4 ± 4.8	41.6 ± 1.5
	-20 m		**-25 m**		**-30 m**	
	Blades	Sheaths	Blades	Sheaths	Blades	Sheaths
July	42.2 ± 0.9	43.2 ± 2.4	41.7 ± 1.1	41.7 ± 3.0	41.5 ± 1.6	39.8 ± 1.6
October	41.3 ± 0.5	41.8 ± 0.4	41.5 ± 0.8	41.3 ± 0.2	40.4 ± 8.0	45.3 ± 7.3
January	40.4 ± 0.2	39.0 ± 1.8	39.4 ± 0.2	38.6 ± 5.8	40.5 ± 0.3	40.2 ± 2.7
April	41.5 ± 1.2	40.0 ± 2.5	41.6 ± 2.7	40.1 ± 5.5	41.0 ± 1.4	40.6 ± 1.3

Blade and sheath production can be estimated for each depth (Table II). The entire leaf production varies between 1 844.3 mg DM.shoot^{-1}.yr^{-1} at -5 m and 736.1 mg DM.shoot^{-1}.yr^{-1} at -30 m (752.2 to 301.4 mg C.shoot^{-1}.yr^{-1}). Rhizome production varies between 59.2 and 34.8 mg DM.shoot^{-1}.yr^{-1} (24.9 to 14.7 mg C.shoot^{-1}.year^{-1}). Total primary production (blades, sheaths and rhizomes) decreases with depth. The mean production, in carbon per shoot, corresponds to 79 % for blades, 17 % for sheaths and 4 % for rhizomes.

Table II: Leaf primary production according to depth at the studied site.

Depth (m)	Mean leaf number.yr^{-1}	Mean blade mass (mg DM)	Blade production (mg DM.shoot^{-1})	Carbon (%)	Blade production (mg C.shoot^{-1})
5	8.6	177.7	1 519.3	40.9	621.5
10	7.5	139.5	1 046.3	41.7	436.8
15	6.6	164.7	1 093.6	41.3	451.4
20	7.0	121.6	851.2	41.4	352.0
25	7.3	124.1	909.7	41.0	373.2
30	6.4	93.8	595.6	40.8	243.1
Depth (m)	Mean leaf number.yr^{-1}	Mean sheath mass (mg DM)	Sheath production (mg DM.shoot^{-1})	Carbon (%)	Sheath production (mg C.shoot^{-1})
5	8.6	38.0	324.9	40.2	130.7
10	7.5	33.1	248.6	40.8	101.5
15	6.6	32.7	217.3	40.7	88.4
20	7.0	25.2	176.3	41.0	72.2
25	7.3	26.1	191.6	40.4	77.4
30	6.4	22.1	140.4	41.5	58.3

The mean total carbon fixation (blades, sheaths and rhizomes) varies between 426.6 and 33.5 g C.m^{-2} with a clear decreasing trend according to depth (Fig. 4).

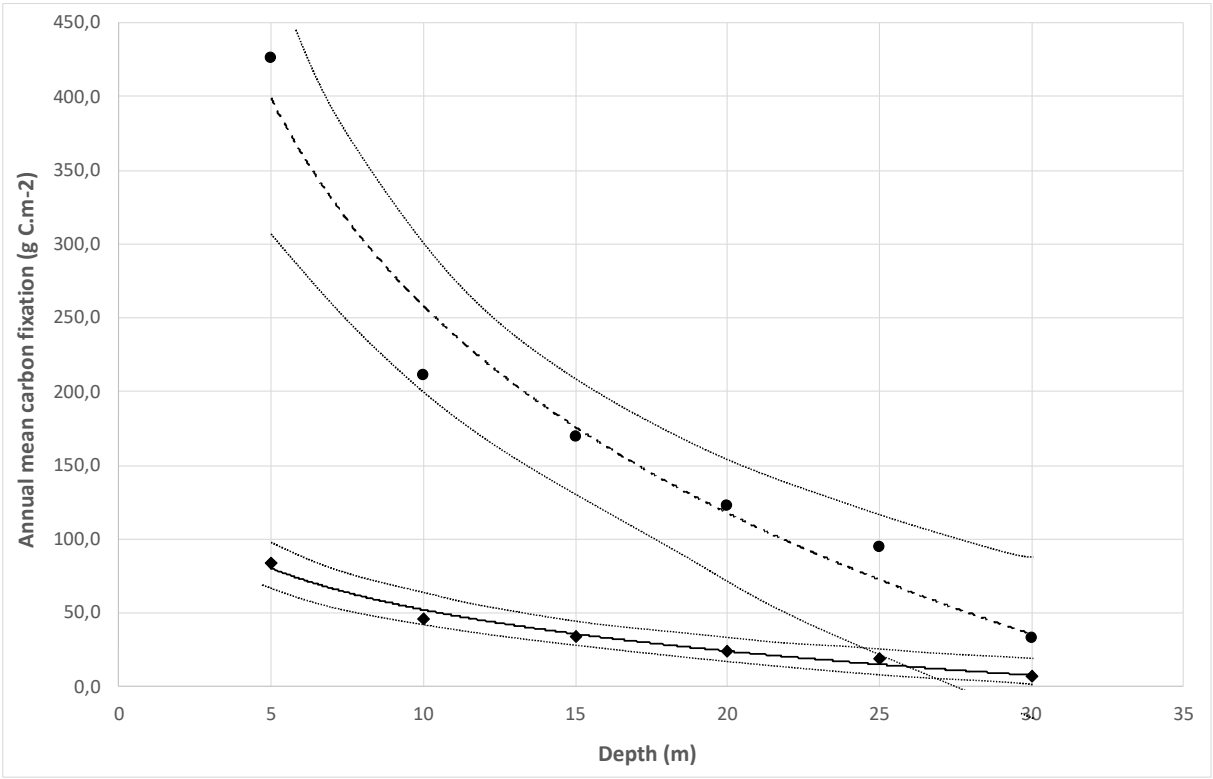

Figure 4: Annual mean carbon fixation (dotted line) and sequestration (solid line) by *P. oceanica* meadow (g $C.m^{-2}$) according to depth; confidence interval (95%) is also reported. Fixation trend curve: y = -202.5 x ln(depth) + 724.6 (R^2= 0.95); sequestration trend curve: y = -40.5 x ln(depth) + 145.5 (R^2 = 0.98).

The mean carbon sequestration (long-term sink in the matte), corresponding to the dead sheath and rhizome tissues, varies between 84.4 and 7.7 g C $.m^{-2}$.

The integration of the carbon fixation and sequestration values over the entire bathymetric range of the *P. oceanica* meadow at the study site makes it possible to estimate the total fixation rate at 22 068 t $C.yr^{-1}$, *i.e.* an average value of 108.0 g $C.m^{-2}.yr^{-1}$, and the sequestration rate at 4 564.7 t $C.yr^{-1}$, *i.e.* an average value of 22.3 g $Cm^{-2}.yr^{-1}$, corresponding to an average depth of 21 m over the entire site (Fig. 5).

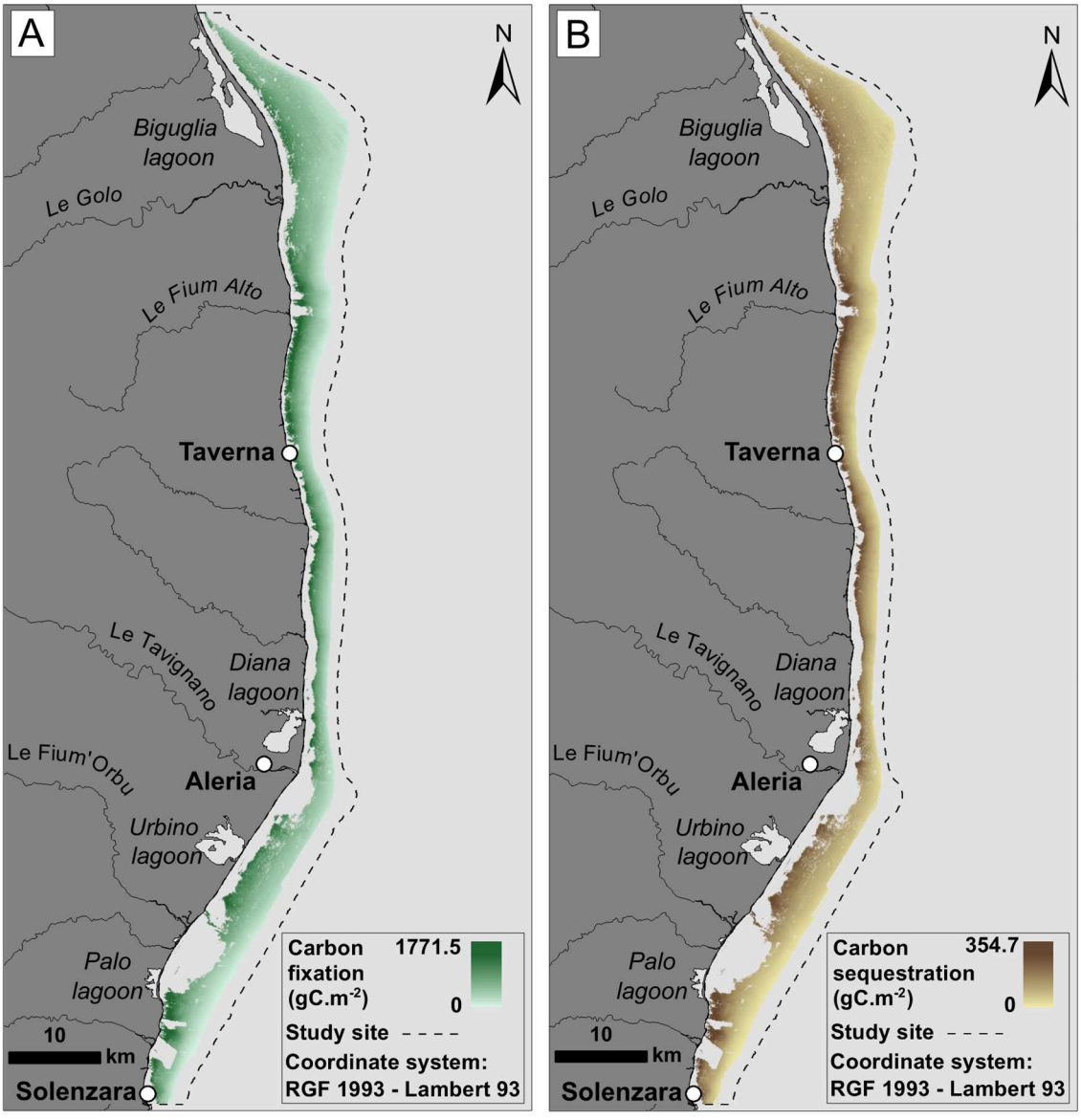

Figure 5: Annual carbon fixation (A) and sequestration (B) by *P. oceanica* meadow (g $C.m^{-2}$) according to depth.

Discussion

Carbon fixation and sequestration by the *P. oceanica* meadow, measured in sector 2 (Fig. 1), corresponds to the sector with the largest extension of this habitat (more than 38% of the areas covered by *P. oceanica* along the Corsican coast; Valette *et al*., 2019). Moreover, recorded values are similar to those measured sporadically in the Bay of Calvi, on the western coast of Corsica (Bay, 1984; Pergent-Martini *et al*., 1994; Vela *et al*., 2006).

Based on the values measured in sector 2, it is therefore possible to extrapolate the carbon fixation and sequestration, by *P. oceanica* meadows, for the entire coast of Corsica (Fig. 4). The areas covered in each sector as well as their average bathymetric extension provide a basis for determining the carbon fixation and sequestration rate (Table III). Total fixation is estimated at 69 275 t C.yr^{-1}, an average of 1.29 t C.ha^{-1}.yr^{-1}, while sequestration rate in the matte (dead sheaths and rhizomes) is estimated at 14 250 t C.yr^{-1}, an average of 0.27 t C.ha^{-1}.yr^{-1} (Table III).

Table III: *P. oceanica* meadow surface area, mean depth (from Valette *et al*., 2019), carbon fixation (-202.5 x ln(depth) + 724.56 and carbon sequestration (-40.46 x ln(depth) + 145.53) in the different sectors. In grey, sector 2, corresponding to the studied site, *= updated in this study; C = carbon.

	P. oceanica surface area (ha)	Mean depth (m)	Mean C fixation (t C.ha^{-1}.yr^{-1})	Carbon fixation (t C.yr^{-1})	Mean C sequestration (t C.ha^{-1}.yr^{-1})	Carbon sequestration (t C.yr^{-1})
Sector 1	4 137	20	1.21	5 005	0.25	1 032
Sector 2	20 425	21*	1.08	22 068	0.22	4 565
Sector 3	3 078	19	1.34	4 116	0.27	846
Sector 4	6 179	16	1.68	10 395	0.34	2 124
Sector 5	3 534	18	1.42	5 001	0.29	1 026
Sector 6	1 430	16	1.70	2 424	0.35	495
Sector 7	2 765	18	1.38	3 804	0.28	781
Sector 8	2 981	18	1.40	4 168	0.29	856
Sector 9	763	20	1.21	927	0.25	191
Sector 10	719	18	1.44	1 038	0.30	213
Sector 11	1 505	18	1.35	2 029	0.28	417
Sector 12	2 940	20	1.21	3 572	0.25	736
Sector 13	1 784	17	1.55	2 766	0.32	566
Sector 14	1 497	19	1.31	1 961	0.27	403

Although the *P. oceanica* meadow in sector 2 covers a very large area, it only allows an average fixation rate of 1.08 t C.ha^{-1}.yr^{-1} and a sequestration rate of 0.22 t C.ha^{-1}.yr^{-1}, the lowest values recorded along the coast of Corsica, because the average bathymetric range of this meadow is the deepest one (-21 m; Table III). This is explained by its deep upper limit due to significant hydrodynamic forces (exposed coast) and of areas unsuitable for *P. oceanica*, near the mouth of coastal rivers (Fig. 1; Pasqualini *et al*., 1998; Boudouresque *et al*., 2012). Conversely, for the sectors where the average bathymetric extension of the meadow is shallower, the carbon fixation rate reaches 1.70 t C.ha^{-1}.yr^{-1} and the sequestration rate 0.35 t C.ha^{-1}.yr^{-1} (sector 4 = East coast of the Natural Reserve of the Strait of Bonifacio; sector 6 = Gulf of Valinco).

The primary production of the *P. oceanica* meadow has been the subject of numerous studies, but they mainly concern the North-Western Mediterranean Sea (Bay, 1984; Buia *et al.,* 1992; Pergent-Martini *et al*., 1994; Cebrian *et al*., 1997; Torricelli & Peirano, 1997; Guidetti & Fabiano 2000; Romero, 2004; Vela *et al.*, 2006), even if some studies are available for other areas of the Mediterranean Sea; Algeria (Boumaza & Semroud, 2000), Croatia (Bakran-Petricioli & Schultz, 2010), Sicily (La Loggia *et al.,* 2004), Turkey (Pergent-Martini *et al*., 1994. These data confirm that, for a continuous meadow, primary production (mg DM.shoot^{-1}) decreases with depth (Fig. 6). However, for a given depth, the values can be highly variable from one site to another (*e.g*. between 310 and 2 250 g DM.shoot^{-1} at -2 m; Boumaza & Semroud, 2000, Vela *et al*., 2006).

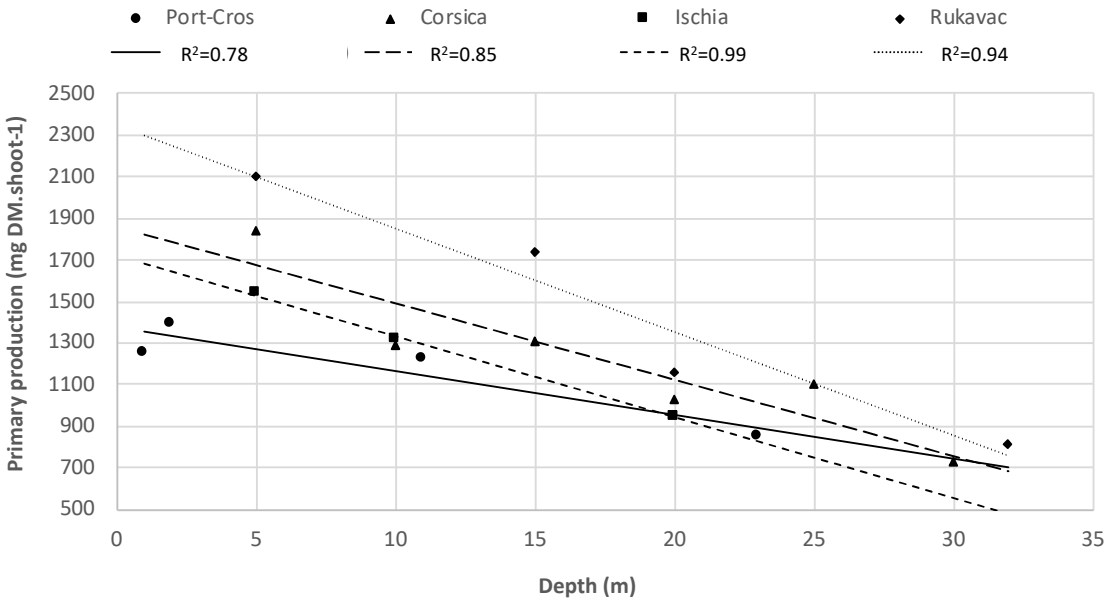

Figure 6: Annual primary production of *P. oceanica* (mg DM.shoot^{-1}) according to depth and site, R^2 = determination coefficient is reported (from Pergent-Martini *et al*., 1994; Bakran-Petricioli & Schultz, 2010 and this study).

The synthesis of a hundred measurements made throughout the Mediterranean Sea and at depths between 0.5 and 32.0 m provides a basis for estimation of the average primary leaf production (in g DM.m^{-2}) according to the depth (Fig. 7). For a depth of 15 m, which corresponds to the average depth of *P. oceanica* meadows in the Mediterranean Sea (mean extension between -2 and -28 m, in UNEP/MAP-RAC/SPA, 2015), annual primary leaf production (blades and sheaths) is estimated at 343 g DM.m^{-2}.

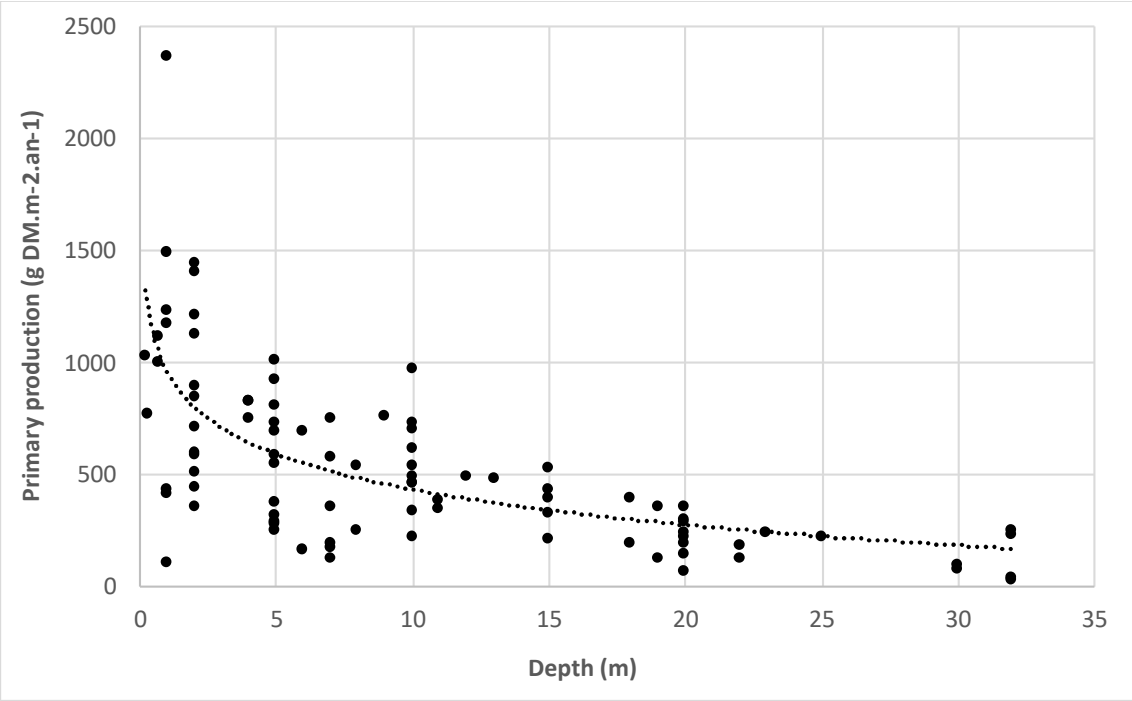

Figure 7: Leaf annual primary production of *P. oceanica* meadow (g $DM.m^{-2}$) according to depth in the Mediterranean Sea (data from: Wittmann & Ott, 1982; Bedhomme *et al*., 1983; Bay, 1984; Thelin & Giorgi, 1984; Wittmann, 1984; Esteban 1989; Romero, 1989; Esteban *et al*., 1990; Buia *et al*., 1992; Pergent-Martini *et al*., 1994; Pergent *et al*., 1997; Torricelli & Peirano, 1997; Zupo *et al*., 1997; Boumaza & Semroud, 2000; Guidetti, 2000; Guidetti *et al*., 2000; Guidetti & Fabiano, 2000; La Loggia *et al*., 2004; Vela, 2006; Vela *et al*., 2006; Bakran-Petricioli & Schultz, 2010; this study). Trend curve: y = -227.2 x ln(depth) + 958.4 (R^2= 0.43).

Carbon concentrations in the leaf tissue of *P. oceanica* show great variability depending on the site (Table IV); thus, they are on average higher in Corsica (38%, Gobert *et al*., 1995; 41.2%, this study), low at Alicante (27.9%, Romero *et al*., 1998) and intermediate at Ischia (30.6 %, Romero *et al*., 1992; 31.3 %, Scartazza *et al*., 2017; 34.9 %, Garrard, 2013). However, the carbon concentration in the tissues does not seem to be significantly impacted by the depth or the season (Garrard, 2013; Table I) although Alcovero *et al*. (2000) highlights a slight variation between winter and spring, probably related to the age of the leaf tissue. The average of the values available in the Mediterranean Sea, for all sites and depths combined, is estimated at 37.8 ± 1.6% for leaf tissue and 42.0 ± 1.1% for rhizomes (Table IV). These values are lower than those measured for terrestrial Magnoliophyta: 47.5% as a mean (Dupouey *et al*., 2000) and 44% in the case of mangrove trees (Bouillon *et al*., 2008).

Table IV: Carbon concentration (%) in leaf tissue and in the rhizomes of *P. oceanica* in the Mediterranean Sea.

Country / Location	Depth (m)	% C in leaves	% C in rhizome	References
Spain / Catalonia	5.0 – 13.0	34.1 - 35.3	35.6	Romero, 1989
Italy / Ischia	20.0	30.6	35.7	Romero *et al*., 1992
Spain	0.5 - 15	38.1		Enriquez *et al*., 1995
France / Corsica	10.0	30.5 - 45.5		Gobert *et al*., 1995
Spain / Alicante	5.0 – 20.0	26.9 - 29.0	38.1 - 38.6	Romero *et al*., 1998
Spain / Catalonia	5.0	30.5 - 35.0	39.0	Alcovero *et al*., 2000
Spain / Murcia	7.5	40.0		Ruiz, 2000

France / Corsica	10.0	32.1		Gobert *et al*., 2005
France / Corsica	11.0	35.6		Leoni et al., 2007
France / Provence	2.0	38.2		Vela, 2006
France / Corsica	2.0	38.7		Vela, 2006
Italy / Sardinia	2.0	38.0		Vela, 2006
Tunisia / Cap Bon	2.0	37.7		Vela, 2006
Tunisia / South	2.0	37.4		Vela, 2006
Italy / Ischia	3.0	33.5 - 35.8		Garrard, 2013
Italy / Ischia	3.0	31.3	38.3	Scartazza et al., 2017
France / Corsica	5.0 - 30.0	37.6 - 43.2	38.0 - 45.8	This study
France / Corsica	8.0 - 37.0	35.1 - 42.4		Gobert unpublished

The average annual carbon fixation and sequestration rate throughout the Mediterranean basin can be estimated from (i) the annual primary leaf production (blades and sheaths) for the integrating depth of -15 m (343 g DM.m^{-2}), (ii) the average proportion of the different tissues produced estimated in this study (blades 79%, sheaths 17%, rhizomes 4%), and (iii) the average carbon concentration of these tissues (37.8 ± 1.6% for leaf tissue and 42.0 ± 1.1% for rhizomes). Thus, the fixation rate of the blades is estimated at 102.4 g C.m^{-2}.yr^{-1}, that of the sheaths at 22.0 g C m^{-2}.yr^{-1} and that of the rhizomes at 5.8 g C m^{-2}.yr^{-1}; *i.e.* a total fixation rate of 130.2 g C m^{-2}.yr^{-1} and sequestration rate (dead sheaths and rhizomes) of 27.8 g C m^{-2}.yr^{-1}.

Based on the available meadow areas for each country, to date (UNEP-MAP-SPA/RAC, 2019), it is possible to make a first evaluation of the amount of carbon fixed and sequestered by the *P. oceanica* meadow each year (Table V). The total amount of carbon fixed is estimated at 3 638 909 tons per year and the amount sequestered at 776 971 tons per year, equivalent respectively to 13 343 878 and 2 849 154 tons per year of CO_2 emission/release equivalent.

Table V: Annual carbon fixation and sequestration by *P. oceanica* meadows in different Mediterranean countries. * UNEP-MAP-SPA/RAC, 2019 ; ** Telesca *et al*., 2015 ; *** Duman *et al*., 2019 ; **** Pergent-Martini *et al*., 2013.

	Available *P. oceanica* surface area (ha)*	Surface mapped (%)**	Estimated *P. oceanica* surface (ha)	Estimated C fixation (t C.yr^{-1})	Estimated sequestration (t C.yr^{-1})
Spain	115 904	100 %	115 904	150 907	32 221
France	87 680	100 %	87 680	114 159	24 379
Monaco	14	100 %	14	18	4
Italy	337 611	100 %	337 611	439 570	93 856
Slovenia	1	100 %	1	1	0
Croatia	31 437	14 %	224 550	292 364	62 425
Bosnia Herzegovina	Not present	100 %*	0		
Montenegro	51	10 %*	512	667	142
Albania	4 803	100 %	4 803	6 254	1 335
Malta	5 860	100 %	5 860	7 630	1 629
Greece	251 010	100 %*	251 010	326 815	69 781
Turkey	39 983	58 %***	68 937	89 756	19 164
Cyprus	3 627	23 %****	15 770	20 533	4 384

Syria, Lebanon, Palestinian territories, Israel	Not present				
Egypt	No data		0		
Libya	1 235	11 %	11 227	14 618	3 121
Tunisia	1 332 815	81 %	1 645 451	2 142 377	457 435
Algeria	4 085	16 %	25 531	33 241	7 098
Morocco	Not present	100 %	0		
Total	**2 216 116**		**2 794 861**	**3 638 909**	**776 974**

Fixation and sequestration of carbon in *P. oceanica* meadows can present a significant part of the CO_2 emissions/releases of the various Mediterranean countries (Table VI). Indeed, even if this fixation represents only 0.61% on average for all Mediterranean countries, it must be borne in mind that (i) seven countries, some of which have a large population (*e.g.* Egypt, Morocco), have not identified any *P. oceanica* meadow, and (ii) that the length of the Mediterranean coast is sometimes very limited compared to the surface area of the country (*e.g*. Slovenia, Turkey, Morocco). However, this fixation may be high for certain countries (*e.g*. 24.6% for Tunisia, 5.6% for Croatia).

Table VI: Carbon fixation in the different Mediterranean countries. Meadow surface area is estimated from the UNEP-MAP-SPA/RAC (2019), 2018 population and national CO_2 emissions from the site http://www.globalcarbonatlas.org/en/CO2-emissions.

	Estimated C fixation (t C)	Estimated CO_2 release* (Mt yr^{-1})	Population (inhabitant)	Estimated CO_2 release (t CO_2.$inhab^{-1}$)	CO_2 fixation by *P. oceanica* (%)
Spain	150 907	268.0	46 692 858	5.74	0.21
France and Monaco	114 178	338.0	64 990 511	5.20	0.12
Italy	439 570	338.0	60 627 291	5.58	0.48
Slovenia	1.3	14.0	2 077 837	6.74	0.00
Croatia	292 364	19.0	4 156 405	4.57	5.64
Bosnia Herzegovina	0	22.0	3 323 925	6.62	0.00
Montenegro	667	2.0	627 809	3.19	0.12
Albania	6 254	4.6	2 882 740	1.60	0.50
Malte	7 630	1.6	439 248	3.64	1.75
Greece	326 815	74.0	10 522 246	7.03	1.62
Turkey	89 756	428.0	82 340 088	5.20	0.08
Cyprus	20 533	7.5	1 189 265	6.31	1.00
Syria	0	28.0	16 945 057	1.65	0.00
Lebanon	0	24.0	6 859 408	3.50	0.00
Ter. Palestinians	0	3.2	4 862 979	0.66	0.00
Israel	0	64.0	8 381 516	7.64	0.00
Egypt	0	239.0	98 423 598	2.43	0.00
Libya	14 618	54.0	6 678 559	8.09	0.10
Tunisia	2 142 377	32.0	11 565 201	2.77	24.55
Algeria	33 241	156.0	42 228 408	3.69	0.08
Morocco		66.0	36 029 093	1.83	0.00
Total (mean)	**3 638 909**	**2 182.9**	**511 844 042**	**4.26**	**0.61**

The large Mediterranean islands deserve special attention because the carbon fixation by *P. oceanica* is higher given the lower population density and the large areas of seagrass beds they shelter (Table VII). The annual carbon fixation is on average 3.1% of CO_2 emissions/releases but can reach almost 14.4% for Corsica. Moreover, the percentage of carbon fixation in comparison with carbon release/emission in the large Mediterranean islands appears higher in the Western basin.

Table VII: Carbon fixation in the large Mediterranean islands. Meadow surfaces are estimated from the report of the UNEP-MAP-SPA/RAC (2019) and from Valette *et al*. (2019); national CO_2 emissions from the site http://www.globalcarbonatlas.org/en/CO2-emissions; * : This study.

	Surface *P. oceanica* (ha)	Carbon fixation (t C.yr^{-1})	Release (t CO_2.yr^{-1})	Fixation by *P. oceanica* (%)
Balearic Islands	63 316	82 437	6 818 687	4.4
Corsica	53 736	69 275	1 763 983	14.4
Sardinia	153 382	199 703	9 143 077	8.0
Sicily	76 000	98 952	27 875 235	1.3
Cyprus	15 770	20 533	7 500 000	1.0
Crete	14 500	18 879	4 465 284	1.6
Total	**396 927**	**516 799**	**59 166 267**	**3.1**

Inter-relationships between variables were investigated by performing a Pearson correlation test (Table VIII); variables correspond to '**Po cover 0-40**' (% *P. oceanica* surface covered/total surface available between 0 and - 40 m in Valette *et al*., 2019), '**C Fixation**' (total island carbon fixation by *P. oceanica* in t C.yr^{-1}), . '**C Sequestration**' (total island carbon sequestration by *P. oceanica* in t C.yr^{-1}), **'% CO_2 Fixed**' (% CO_2 fixed by *P. oceanica*/CO_2 released in t CO_2.yr^{-1}) and '**CO_2 Release Inhab**' (total island CO_2 released per inhabitant in t CO_2.yr^{-1}.inhab^{-1} according to http://www.globalcarbonatlas.org/en/CO2-emissions).

The areas covered by the *P. oceanica* meadows between 0 and -40 m are significantly greater for the islands located to the north (r = 0.941; p-value<0.01) and to the west (r = 0.904; p-value<0.05) of the Mediterranean Sea (*i.e.* Sardinia, Corsica, Balearic Islands). Conversely, CO_2 emissions per capita/inhabitant are negatively correlated with latitude (r = 0.863; p-value<0.05) reflecting higher CO_2 emissions for the inhabitants of the islands in the south of the Mediterranean basin (*i.e.* Cyprus, Crete). Thus, the northwestern Mediterranean islands, characterized by lower CO_2 emissions per capita/inhabitant and greater coverage of *P. oceanica* meadows within the bathymetric range from 0 to -40 m, appear as sectors where the ratio CO_2 fixed / CO_2 released is the highest (r = 0.880; p-value<0.05)
Finally, the carbon sequestered by *P. oceanica* meadows in the matte is significantly correlated with the fixation of carbon produced by the plant (r = 0.979; p-value<0.001).

Table VIII: Pearson's correlation matrix between geographical, environmental and carbon variables. Level of significance: *p≤0.05, **p≤0.01, ***p≤0.001; NS, p≥0.05; Significant correlations in bold (r value).

Variables	**Longitude**	**Latitude**	**Po cover 0-40**	**C Fixation**	**C Sequestration**	**% CO_2 Fixed**	**CO_2 Release Inhab**
Longitude		**-0.854**	**-0.904**	-0.574	-0.621	-0.529	0.720

Latitude	*		**0.941**	0.544	0.547	**0.880**	**-0.863**
Po cover 0-40	*	**		0.473	0.511	0.794	-0.681
C Fixation	NS	NS	NS		**0.979**	0.316	-0.594
C Sequestration	NS	NS	NS	***		0.312	-0.523
% CO_2 Fixed	NS	*	NS	NS	NS		-0.673
CO_2 Release Inhab	NS	*	NS	NS	NS	NS	

Carbon fixation by *P. oceanica* is high with an average of 1 302 t C $ha^{-1}.yr^{-1}$. Even if the areas covered by *P. oceanica* meadows are smaller than those of other terrestrial ecosystems, this ecosystem represents around 4% of the areas covered by forest ecosystems in all Mediterranean countries (FAO & Plan Bleu, 2018) and more than 20% for the six large Mediterranean islands (FAO & Plan Bleu, 2018).

Morever, the major advantage of the *P. oceanica* meadow lies in its capacity to store carbon in soil from centuries to millennia. The average carbon stock found in the matte, resulting from the accumulation of 21% of annual primary production, varies between 40 and 237 kg $C.m^{-2}$ (Romero *et al*. 1994, Mateo *et al*. 1997, Serrano *et al*., 2012; 2014). These values are similar or higher than those measured in several terrestrial ecosystems considered to be efficient in carbon storage such as peatlands (120 kg $C.m^{-2}$; Warner *et al*., 1993), wetlands (13-73 kg $C.m^{-2}$; Laffoley & Grimsditch 2009) and the boreal forests (9-34 kg $C.m^{-2}$; Serrano *et al*. 2014) and Mediterranean forest (5.7 kg $C.m^{-2}$; FAO & Plan Bleu, 2018).

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