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Review

Mediterranean seagrass (*Posidonia oceanica*) loss between 1842 and 2009

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ABSTRACT

We compiled published data in peer-review articles and grey literature reports, which we appended with our own data, to assess the changes in areal extent, cover and shoot density that *P. oceanica* meadows have experienced between years 1842 and 2009 in the Mediterranean basin. Our results demonstrate an overall tendency towards decline of the areal extent, cover and shoot density of *P. oceanica* meadows during the last 50 years, the period with the largest availability of records. Available estimates indicated that between 13% and 50% of seagrass areal extent of *P. oceanica* in the Mediterranean basin appear to be lost, and that the remaining meadows of the Mediterranean may have thinned shoot density by 50% for the last 20 years and have became more fragmented. Considering the changes quantified in *P. oceanica* areal extent, cover and density, about 6.9% of the potential *P. oceanica* vegetation would have been lost annually over the last 50 years. The loss of *P. oceanica* meadows in the Mediterranean may have lead to a substantial (between 11% and 52%) reduction of the capacity of this key coastal ecosystem to sequester carbon in the last 50 years, hence reducing the carbon sink capacity of the entire Mediterranean Sea. The major causes of *P. oceanica* loss were widespread local disturbances, but recently, global disturbances, such as climate change and the spread of invasive exotic species, were also seriously threatening *Posidonia* meadows in the Mediterranean. These findings urgently call for implementation of management measures aiming at mitigating coastal deterioration by combining local and global actions.

Contents

1. Introduction

Anthropogenic pressure on the Mediterranean coastal zone has increased rapidly during the second half of 20th century, as the number of residents and tourists almost doubled between 1970 and 2000 (Benoit and Comeau, 2005). Consequently, the Mediterranean coastal zone is suffering intense transformation: 40% of the Mediterranean coastline had been built over by 2000 (Benoit and Comeau, 2005), coastal aquaculture has grown greatly (Benoit and Comeau, 2005) and nitrate concentration in the western Mediterranean has increased by 0.5 per cent per year between 1975 and 1995 (Benoit and Comeau, 2005). This increasing human pressure has prompted the deterioration of the Mediterranean coast as reflected by, among other symptoms, eutrophication, decrease in water clarity, erosion, and losses of coastal habitats and biodiversity (Benoit and Comeau, 2005).

The key ecosystem component, *Posidonia* meadows, acts as a sensitive recipient as well as an indicator of these impacts (e.g. Martínez-Crego et al., 2008). *Posidonia oceanica* is a Mediterranean endemic seagrass (marine angiosperm) species forming lush, extensive meadows between 0 and 45 m depth around the

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Mediterranean coast. *Posidonia* meadows provide important services, as they are important carbon sinks (e.g. Duarte et al., 2005; Mateo et al., 1997), stabilize the sediment, protect the coastline from erosion, support biodiversity and enhance living resources (Barbier et al., 2011). *P. oceanica* is exceptional in that it is arguably one of the longest lived species, with individual shoots living up to 50 years (Marbà et al., 2002) and clones aged several millennia (Arnaud-Haond et al., 2012), and ranks among the slowest growing (1–6 cm per year) plants (Marbà and Duarte, 1998). *P. oceanica* meadows are highly vulnerable to coastal deterioration; excess nutrient and organic inputs, coastal erosion and mechanical impacts (e.g. fish trawling, coastal constructions, dredging), and climate change lead to rapid losses of *P. oceanica* (e.g. Boudouresque et al., 2009; Díaz-Almela et al., 2008a; Díaz-Almela et al., 2009; Jordà et al., 2012) throughout the Mediterranean. The rapid spread of invasive species in the Mediterranean is also threatening *P. oceanica* meadows (Williams, 2007; Marbà et al., 2014).

As a result of the multiple stresses experienced by *P. oceanica* meadows, their decline has been reported across the entire Mediterranean basin (e.g. Boudouresque et al., 2009). These observations have increased awareness of the vulnerability of this key ecosystem and have lead to efforts to assess their conservation status in several Mediterranean areas (Marbà et al., 2013a). However, an evaluation of the rates of change of the extension and abundance of *P. oceanica* meadows in the entire Mediterranean basin for the last 50 years is lacking, therefore the extent and rate of decline along the Mediterranean area remains a matter of speculation.

Here, we examine the trajectory (i.e. expanding, declining, steady-state) and quantify the rates of change of the areal extent, cover (i.e. percentage of seafloor covered by seagrass) and shoot density of *P. oceanica* meadows across the Mediterranean basin between 1842 and 2009. In addition, we provide an overall estimate of *P. oceanica* vegetation loss for the Mediterranean. Finally, we examine the type of pressures nearby the *P. oceanica* meadows to identify the major threats to Mediterranean seagrass meadows during the studied period. We do so, by compiling published data in peer-review articles and grey literature reports amended with our own data.

2. Methods

We compiled available data published in peer-review articles and grey literature reports until year 2009 and combined them with our own unpublished data. We searched for data with the search engine ISI Web of Knowledge, using the keywords *P. oceanica* AND (regression OR decline OR progression OR recovery OR status OR cartography OR limits OR cover OR density OR biomass OR dynamics), and furthermore conducted a back search of cited papers. The full dataset compiled is available at Digital CSIC (Marbà et al., 2013b).

The type of data gathered included information about characteristics of the study conducted (i.e. year or period of years of the study, site, country, water depth), information about seagrass meadows (i.e. areal extent, depth of deep and shallow limit, cover, shoot density, meadow status (decline, expansion, steady-state), rate of change, Index of Conservation) and types of coastal pressures present. The data set includes both qualitative and quantitative data, since it contains studies where changes in seagrass meadow areal extent, cover and/or density are identified from expert judgement as well as studies that quantified the magnitude and rates of the changes reported. The Index of Conservation (IC, Moreno et al., 2001; a variation of the Index of Alteration IA proposed by Sánchez-Poveda et al., 1996), which is related to the proportional abundance of living *P. oceanica* to dead matte and living *P. oceanica*, provided by the studies, was calculated as:

$$\mathrm{IC} = \%\ \text{seagrass area}/(\%\ \text{dead matte area} + \%\ \text{seagrass area})$$

and thus the period when the change occurred was not determined.

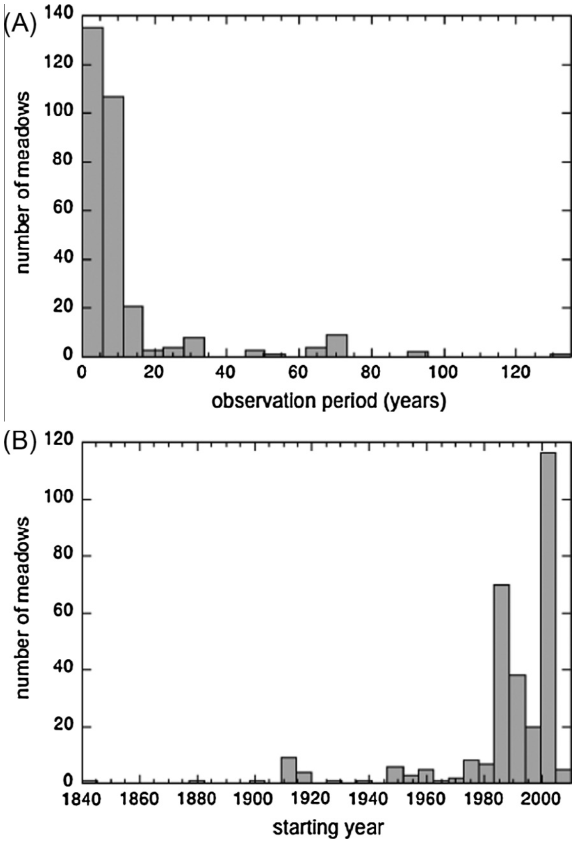

Fig. 1. Number of meadows of *Posidonia oceanica* that have been assessed for different duration of periods (A) and the year when the observations started (B).

The duration of the time interval over which *P. oceanica* status was assessed was reported by 54% of the studies compiled. The length of the observational period ranged between 1 year and 130 years (Fig. 1), although most meadows were monitored over less than one decade (median duration of 6 years, Fig. 1A) and after year 1993 (Fig. 1B). *P. oceanica* meadow status was first assessed on the basis of changes in areal extent, with a median central year of surveys in year 1987 (Table 1), whereas the median central years of assessments of meadow status using cover and shoot density approaches were 2004 and 2001, respectively (Table 1). The duration of the observational period to assess *P. oceanica* meadow status also differed depending on the approach used, tending to be shorter for assessments based on shoot density than for those comparing areal extent (Table 1).

The rates of change were calculated when the time frame of the study was reported. The absolute rate of change (ABS) of areal extent (ha yr^{-1}), depth of shallow and deep meadow limits (m yr^{-1}), % cover (% cover yr^{-1}) or shoot density (shoots $\mathrm{m}^{-2}\ \mathrm{yr}^{-1}$) was calculated as:

$$\mathrm{ABS} = (N_t - N_0)/t$$

where N_t is the area (ha), depth of meadow limits (m), cover (% cover) or shoot density (shoots m^{-2}) at the end of the study, N_0 the area, depth limits, cover or shoot density at the beginning of the study, t the observation period (yr). Absolute rate of change to some extent, depends on the initial abundance, which for shoot

Table 1
Range, mean, standard error of the mean (±SE), and median of mid year and duration of the observation period when changes in areal extent, cover and shoot density in *Posidonia oceanica* meadows have been assessed. The number of assessed meadows is also indicated.

	Areal extent	Cover	Shoot density
Number of meadows	70	40	170
Mid year of observation period			
Range	1908–1998	1966–2004	1985–2005
Mean ± SE	1976 ± 2	1998 ± 2	1998 ± 0.5
Median	1987	2004	2001
Duration of observation period (years)			
Range	2.0–131.0	2.0–30.0	0.3–29.0
Mean ± SE	27.4 ± 3.5	9.5 ± 1.4	4.9 ± 0.3
Median	10.0	6.0	4.0

density and cover largely couples to water depth (Lopez y Royo et al., 2010). Conversely, the relative rates of change (μ, % yr^{-1}) of areal extent or shoot density are independent from initial abundance (Marbà et al., 2005) and were quantified as:

$$\mu = \ln(N_t/N_0)/t$$

Additionally, the database includes 62 estimates of relative change in shoot density that were calculated using retrospective techniques (Duarte et al., 1994), which accounted for 81.6% of all estimates of relative change in shoot density compiled. We categorized the meadows as declining (final area < 90% of initial area, net% cover absolute change < −10, or $\mu_{density} < -5\%\ yr^{-1}$), increasing (final area > 110% of initial area, net cover change > 10% yr^{-1}, or $\mu_{density} > 5\%\ yr^{-1}$) or without detectable change (final area within < 90% of initial area, −10% yr^{-1} < net cover change < 10% yr^{-1}, or $-5\%\ yr^{-1} < \mu_{density} < 5\%\ yr^{-1}$) following Waycott et al. (2009) for area and Calleja et al. (2007) for shoot density criteria.

3. Results

The state (i.e. decline, expansion, steady-state) of *P. oceanica* meadows, until 2009, was reported for 519 meadows. The first record of *P. oceanica* mapping dated from 1842, more than one century before initiation of the development of the Mediterranean coastal areas in the 1960s. Efforts to evaluate the status of *P. oceanica* meadows started in 1962, and the number of meadows assessed increased since at an average rate of 13.0 ± 0.5% yr^{-1} ($R^2 = 0.95$, $p < 0.0001$, Fig. 2). However, the number of meadows assessed per year for the last two decades decreased to 5 ± 0.2% yr^{-1} ($R^2 = 0.97$, $p < 0.0001$, Fig. 2). Most (43.2%) studies assessed meadow state by examining the areal extent of *P. oceanica* (spatial scale of hectares), followed by the evaluation of shoot density (spatial scale of square meter, 42.4%) and that of percentage of seafloor covered by *P. oceanica* (spatial scale of tens of square meter, 17.1%, Fig. 2). The approach used to assess the meadow state was not specified in 4% of the studies whereas 6% of the studies used more than one approach.

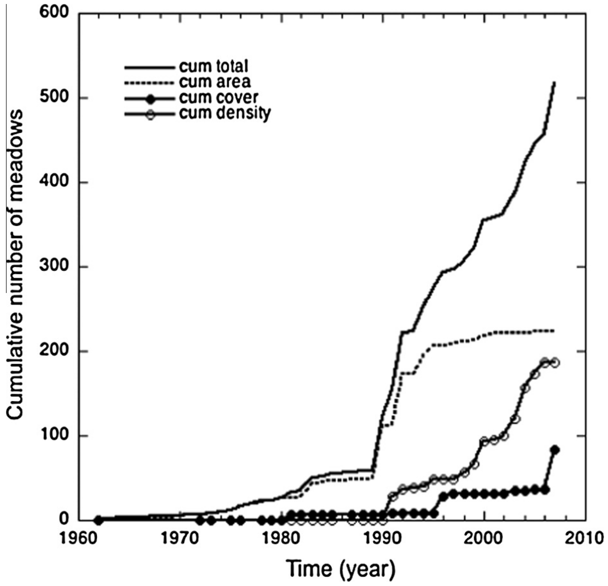

Fig. 2. Cumulative number of *Posidonia oceanica* meadows where the state (i.e. decline, steady-state, expansion) has been assessed since 1960 by examining meadow areal extent, cover and/or shoot density.

Knowledge on the state of *P. oceanica* meadows was strongly biased towards the Western Mediterranean; observations in this region accounting for 96.8% of all reports (Fig. 3). Two thirds (62.0%) of the meadows assessed had experienced declines in areal extent (including declines both at the shallow and deep limits), cover and/or shoot density (Figs. 3 and 4). Losses exceeded 50% of areal extent in 36 meadows, of cover in 12 meadows and of density in 6 meadows, accounting in total for 10.6% of all studied meadows. Four *P. oceanica* meadows (0.8% of all studied meadows) were entirely lost. Only 26.6% of the studied meadows were in steady-state, whereas 11.4% expanded (Figs. 3 and 4).

The rate of change of areal extent (including change in depth of meadow limits) or shoot density of *P. oceanica* meadows was only quantified in 38% of the reports on meadow status, i.e. those where areal extent, cover and/or shoot density estimates were quantified at the beginning and end of a known time period. These studies documented, since year 1842, a net loss of 7277.3 ha of mapped *P. oceanica* meadows, accounting for 12.9% of the entire mapped *P. oceanica* areal extent (56,545 ha). In addition, 1608 ha of *P. oceanica* meadows were degraded. Declining *P. oceanica* meadows lost, on average, −27.38 ± 9.93 ha yr^{-1} (Table 2), although the median absolute rate was −3.83 ha yr^{-1} (Table 2).

The average absolute rate of increase of meadow areal extent, for the 10% of meadows expanding, was 40-fold slower that the average rate of loss of the declining meadows (Table 2). Owing to the fact that there was a greater number of meadows losing rather than gaining areal extent, and that loss rates were much faster than gain rates, the median overall relative rate of change of *P. oceanica* areal extent was −1.74% yr^{-1} (Table 2), pointing to an overall decline of *P. oceanica* areal extent over the last century.

In addition to the changes in total areal extent of the *P. oceanica* meadows, other investigations reported changes in the water depths of shallow and deep limits of the meadows over the last century. Mostly after year 1990, the meadows extended, on average, between 6.2 ± 0.42 m ($n = 109$, shallow limit) and 22.6 ± 0.82 m ($n = 125$, deep limit) deep. A total of 42 studies reported changes in the shallow limit of the meadows, and 39 for the deepest limit. The shallow limit of most (26 out of 42) *P. oceanica* meadows evaluated regressed towards deeper waters, whereas in few meadows (8 out of 42) it progressed towards the coastline. In only 19% (8 out of 42) of the evaluated meadows the depth of their shallow limit was stable. Few studies quantified the magnitude and rate of change of the shallow limit of the meadow (Table 3), but the overall change in water depth of shallow limits of the meadow during the study period was, on average, −1.7 ± 0.4 m (Table 3), and it occurred at an average absolute rate of −0.04 ± 0.1 m yr^{-1} (Table 3). Similarly, most (33 out of 39) meadows studied also regressed at their deep limit during the study period, whereas deep limits remained in steady state in 8 meadows and progressed in 8 meadows. The few estimates available indicated that since they were first assessed *P. oceanica*

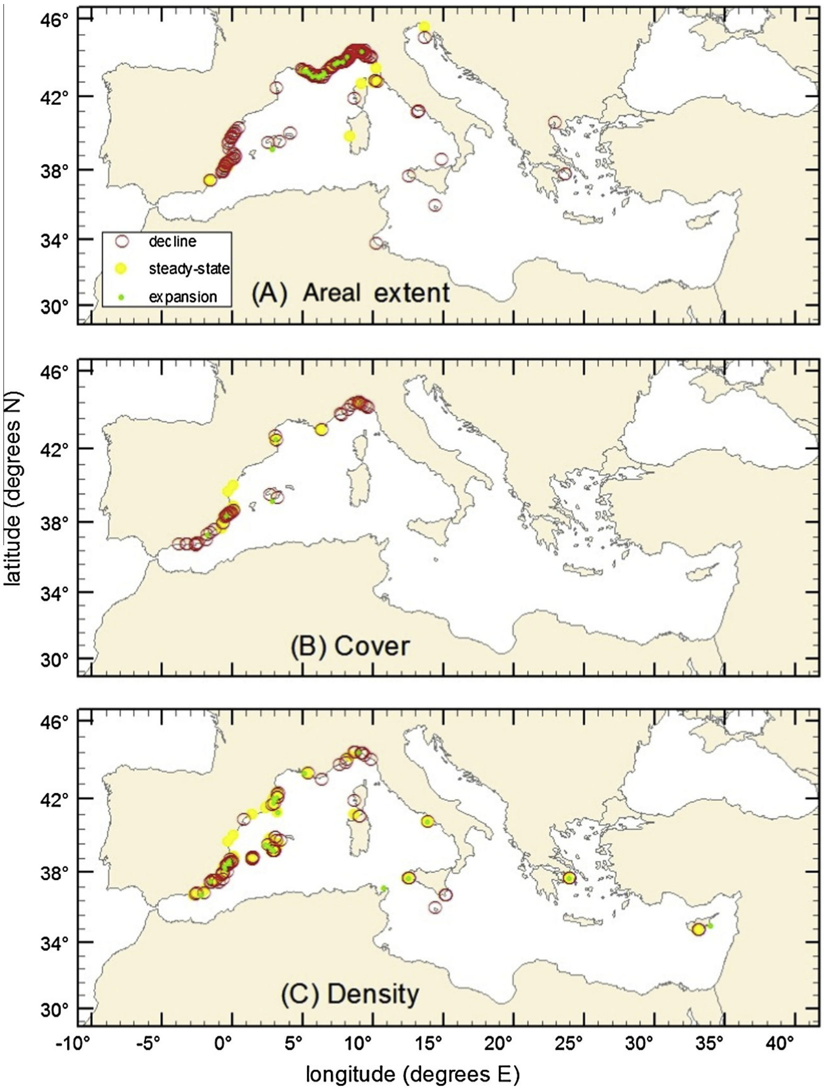

Fig. 3. Distribution of all *Posidonia oceanica* meadows that have been reported to be declining, in steady-state, and expanding by assessing meadow areal extent, cover and shoot density.

meadows have reached maximum colonisation depths, on average, 6.8 ± 2.9 m shallower by the end of the study (Table 3). For the few meadows where estimates were available, maximum colonisation depth of *P. oceanica* declined at an overall absolute rate of 0.61 ± 0.29 m yr^{-1} (Table 3), 10-fold faster than the overall rate of regression at their shallow limit. Given the average meadow depth range between shallow and deep limits of 16.4 m and the overall median net absolute vertical change of -0.35 m yr^{-1}, the relative total vertical rate of change was -2.2% yr^{-1}.

The percentage of *P. oceanica* cover and shoot density in the areas where the meadow was not lost also exhibited changes during the last decades (Fig. 3). The rate of absolute change of the percentage of seagrass cover was available for only 16 *P. oceanica* meadows. Half of the estimates revealed a loss in cover at an average rate of -2.67 ± 0.99% yr^{-1}. Cover was in steady state in 44% of the meadows and the single meadow where cover increased did so at a rate of 1.83% cover yr^{-1} (Table 2). Hence, the overall rate of change of *P. oceanica* cover in the Mediterranean indicated a net decline of cover at, on average, -1.22% yr^{-1} (Table 2).

Changes in shoot density were quantified in 81 occasions as absolute and in 153 occasions as relative changes (Table 2). The shoot density in most (43%) meadows thinned at an average absolute rate of -56.38 ± 7.57 shoots m^{-2} yr^{-1} and at a median relative rate of -13.96% yr^{-1} (Table 2). Shoot density increased in 16% of the meadows at an absolute rate of 29.90 ± 11.51 shoots m^{-2} yr^{-1} and at a median relative rate of 10.63% yr^{-1} (Table 2). Given the greater number of meadows experiencing declines in shoot density than increasing shoot density or in steady-state, and the faster loss compared to gain rates of shoot density, the overall median relative rate of shoot density change was -4.20% yr^{-1} (Table 2), demonstrating an overall thinning trend of *P. oceanica* meadows during the study period.

P. oceanica declines were attributed to human physical impacts in two thirds (67.6%) of investigated meadows, involving seawater turbidity and siltation, coastal erosion, anchoring, fish trawling, coastal works, beach refilling, climate warming and thermal and desalination seawage. Coastal eutrophication, derived from urban, industrial and aquaculture seawage, impacted 30% of the investigated meadows (Fig. 5), whereas biological impacts, represented by damages from invasive seaweed species, were recorded in 2.4% of the meadows investigated (Fig. 5). Seagrass loss in 39% of the declining meadows was attributed to more than one single pressure.

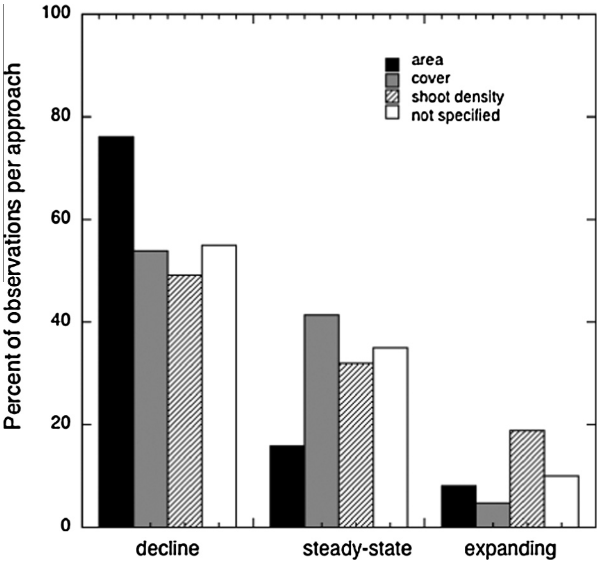

Fig. 4. Percentage of observations of *Posidonia oceanica* meadows declining, expanding, or in steady state in the Mediterranean Sea during the last century assessed by examining meadow areal extent (black bars), cover (grey bars), shoot density (hatched bars) or without indicating the assessment approach (white bars).

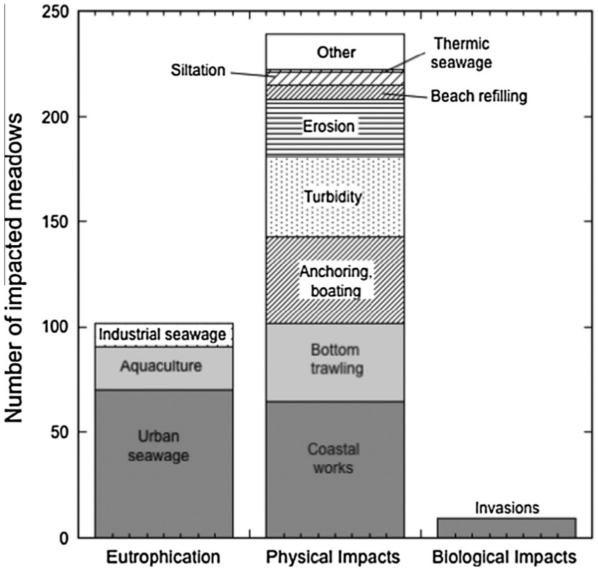

Fig. 5. Pressures identified as causes of *Posidonia oceanica* declines. The graph shows the number of meadows impacted by each pressure.

Table 2
Absolute (ha yr^{-1}, for areal extent; % cover yr^{-1} for cover; shoots m^{-2} yr^{-1}, for density) and relative (% yr^{-1}) annual rates of loss, gain and overall estimates of areal extent, percentage cover and shoot density in *Posidonia oceanica* meadows in the Mediterranean Sea. The number of estimates and the percentage of estimates of meadows in each state are also provided.

State	Number of estimates	% Estimates[*]	Absolute rate		Relative rate			
			Mean	SE	Median	Mean	SE	Median
Areal extent								
Steady-state	0	0						
Loss	18	78	−27.38	9.93	−3.83	−2.95	0.65	−2.06
Gain	5	22	0.69	0.62	0.02	1.31	0.49	0.97
Overall	23		−21.28	8.11	−2.21	−2.02	0.63	−1.74
Cover								
Steady-state	7	44	0.002	0.17	−0.16			
Loss	8	50	−2.67	0.99	−1.55			
Gain	1	6	1.83		1.83			
Overall	16		−1.22	0.62	−0.80			
Density								
Steady-state	33 (52)[**]	41 (34)[**]	−20.35	19.04	−1	0.6	0.43	−0.65
Loss	35 (72)[**]	43 (47)[**]	−56.38	7.57	−45	−43.46	9.49	−13.96
Gain	13 (29)[**]	16 (19)[**]	29.90	11.51	27.50	15.57	2.21	10.63
Overall	81 (153)[**]		−27.51	9.07	−4.83	−15.9	4.57	−4.20

[*] Relative to the total number of estimates per approach (i.e. area, cover, density).

[**] Number of absolute (outside brackets) and relative (inside brackets) estimates and% within approach.

Table 3
Average, standard error (SE) and median total change and absolute rate of change of depth of the shallow and deep limit of *Posidonia* meadows in the Mediterranean during the last decades. Total change and rates of change are estimated for declining, expanding and overall depth limits assessed. Data not available is indicated (nd).

State	Total change (m)				Absolute rate of change (m yr^{-1})			
	Number of estimates	Mean	SE	Median	Number of estimates	Mean	SE	Median
Shallow limit								
Steady-state	2	0.00	0.00	0.00	2	0.00	0.00	0.00
Loss	9	−2.06	0.32	−2.50	9	−0.05	0.01	−0.04
Gain	0	nd	nd	nd	0	nd	nd	nd
Overall	11	−1.68	0.36	−1.50	11	−0.04	0.01	−0.04
Deep limit								
Steady-state	1	0.00		0.00	1	0.00		0.00
Loss	8	7.63	3.11	4.75	8	0.68	0.32	0.36
Gain	0	nd	nd	nd	0	nd	nd	nd
Overall	9	6.78	2.87	3.00	9	0.61	0.29	0.31

Table 4
Maximum and minimum estimates of current *Posidonia oceanica* areal extent, % of potential extension lost and current rate of carbon sequestration by *Posidonia oceanica* meadows in the entire Mediterranean Basin.

	Estimated current areal extent (km^2)	% Areal extension loss	Carbon sequestration rate (gCO$_2$ m^{-2} yr^{-1})[***]	Carbon sequestration rate by *P. oceanica* in the Mediterranean (Tg CO$_2$ yr^{-1})
Max	43,550[*]	13	630	27
Min	31,040[**]	38	630	20

50,000 km^2 of potential initial areal extent of *Posidonia oceanica* meadows in the Mediterranean (Bethoux and Copin-Montégut, 1986).
[*] Calculated from the overall% of net change in areal extent (−12.9%) from mapped meadows since 1842.
[**] calculated using the overall median rate of areal extent change (−0.017 yr^{-1}, Table 2) and the average observational time period for areal extent status (27.4, Table 1).
[***] From Duarte et al., 2010.

4. Discussion

The results obtained, indicate that *P. oceanica* meadows have been declining, particularly since the second half of the 20th Century, as it has occurred for seagrass meadows worldwide (Waycott et al., 2009). This assessment was conducted on the basis of reported measurements of seagrass changes, which were only available for a sample of *P. oceanica* meadows in the Mediterranean encompassing about 1% of the estimated potential *P. oceanica* areal extent. The percentage of the areal extent lost relative to the total area mapped accounts for a net loss of 12.9% of the initial extension, about half of that reported for seagrasses globally (Waycott et al., 2009). However, the overall relative rate of change of *P. oceanica* areal extent of −1.74% yr^{-1} (Table 2), mostly quantified after 1977, is almost twice of that estimated for seagrasses globally (−0.9% yr^{-1}, Waycott et al., 2009). Assuming that the quantified losses of *P. oceanica* areal extent, mostly in NW Mediterranean, have occurred at similar rates across the entire Mediterranean basin, and considering that 50,000 km^2 of coastal Mediterranean seafloor between 0 and 40 m could have been covered with *P. oceanica* in the past (Bethoux and Copin-Montégut, 1986), the current overall *P. oceanica* areal extent could range between 31,000 km^2 and 43,500 km^2 (Table 4). Our estimates of the overall rates of change of *P. oceanica* areal extent reveal that between 13% and 38% of potential initial seagrass area may have been lost since 1960 (Table 4). The losses of *P. oceanica* areal extent may be considered irreversible at human-life time scales because the biological characteristics of the species (i.e. slow growth rates and low production of sexual recruits) prevent rapid re-colonisation of bare sediments (Díaz-Almela et al., 2008a; Diaz-Almela et al., 2008b; Kendrick et al., 2005). The lack of information on the state of *P. oceanica* meadows along the Eastern Mediterranean and Northern African coasts prevents the assessment of differences in seagrass conservation status among Mediterranean regions.

The loss of *P. oceanica* areal extent involves a compression of their depth range, as the meadows have experienced regression both at shallow limit, by a median of 0.04 m yr^{-1}, and at their deep limit, by 0.31 m yr^{-1}, representing a relative loss rate of about −2.2% yr^{-1}, similar to that calculated from areal extent losses (−1.74% yr^{-1}). The regression of the shallow and deep limits involves different drivers. Most (57%) reported declines of deep limits of *P. oceanica* meadows occurred in coastal areas with organic and nutrient seawage inputs. The maximum seagrass colonisation depth is closely related with, and can be empirically predicted from, light extinction coefficient in the water column (Duarte et al., 2007). The maximum seagrass colonisation depth is located where about 10% of the surface incident light reaches the leaves (Duarte, 1991). Using the empirical relationship described by Duarte et al. (2007) the net change in the depth of the deep limit estimated in this study would correspond to an increase in the light extinction coefficient in these areas by 0.013 m^{-1}, and thus a substantial decrease (18%) of seawater transparency. Hence, the overall trend of regression of *P. oceanica* meadows at their deep limit suggests a deterioration of the environmental quality of Mediterranean coast, translated into a decline in water transparency. Other pressures, such as bottom trawling, have also been identified to impact the deep limit of *P. oceanica* meadows in 24% of the reports compiled. Conversely, the regression of the meadow at the shallow limit involves different drivers. In particular the regression of *P. oceanica* meadows at their shallow limit is caused by physical perturbation, either siltation or, more commonly, erosion associated with coastal development, such as building of marinas, peers, breakwaters and other structures (e.g. Astier, 1984; Boudouresque et al., 2000; Medina et al., 2001).

In addition to the loss of the areal extent of *P. oceanica* meadows, the remaining *P. oceanica* vegetation has thinned over the last decades, as revealed by the overall loss of shoot density and seagrass cover (Table 2). Our estimates indicate that since 1990, when shoot density started to be evaluated (Fig. 2), shoot density in *P. oceanica* meadows has decreased, on average, by 50%. Similarly, the extension of bare area within the meadows has increased by, on average, 17%. These results reveal a substantial loss of *P. oceanica* vegetation both in terms of areal extent as well as in cover and shoot density since the second half of 20th Century. Combining the nested array of the components of net change (Table 2), i.e. overall rate of change of areal extent ($\mu_{\text{areal extent}}$) and overall change in cover (μ_{cover}) within the meadows and overall change in density ($\mu_{\text{shoot density}}$) within areas still covered, we estimated the compounded loss of *P. oceanica* density or biomass as,

$$\text{Compounded loss} = \mu_{\text{areal extent}} + \left[\mu_{\text{cover}} * (1 - (\mu_{\text{areal extent}}/100))\right] + \left[\mu_{\text{shoot density}} * (1 - ((\mu_{\text{areal extent}}/100) * (1 - (\mu_{\text{cover}}/100))))\right]$$

The compounded loss of *P. oceanica* density or biomass is estimated at −6.9% yr^{-1} in the Mediterranean, representing a steep decline in this key ecosystem.

The causes of the observed *P. oceanica* declines encompass eutrophication, physical impacts and biological agents (Fig. 5) often derived from pressures acting simultaneously. Most declines of *P. oceanica* reported for the last decades resulted from local impacts, whereas meadow decline has been seldom and, only recently, attributed to pressures occurring at the regional scale, such are the invasion of alien species, climate warming and, to some extent, coastal erosion (Fig. 5). While efforts in Europe to reduce the local impacts to *P. oceanica* meadows have increased over the last two decades through improved coastal seawater quality (e.g. implementation of the EU Water Framework Directive) and implementing seagrass conservation measures (e.g. EU Habitat Directive, legislation at national and regional level), climate change and other global pressures, reflected for instance in growing maritime traffic, are emerging as threats to seagrass ecosystems (e.g. Benoit and Comeau, 2005; Marbà and Duarte, 2010). Hence, efforts to conserve *P. oceanica* meadows should also encompass polices addressed to mitigate and regulate global pressures; local action alone, while essential, does not suffice to ensure the conservation of *P. oceanica* meadows (e.g. Jordà et al., 2012).

The important net loss of areal extent of *P. oceanica* meadows in the Mediterranean basin implies that the services they provide should have declined since the second half of 20th Century as well. Recent reviews (Duarte et al., 2010; Kennedy et al., 2010) demonstrate that seagrass meadows sequester between 580 and 680 $gCO_2\ m^{-2}\ yr^{-1}$ due to seagrass community metabolic rates and the high efficiency of seagrass meadows at capturing and burying suspended particles in the water column. Accordingly, at present, *P. oceanica* in the Mediterranean basin would be sequestering annually between 20 and 27 Tg CO_2 (Table 4), representing between 62% and 87% of that sequestered before 1960. Hence, the role of *P. oceanica*, the most important natural carbon sink in the Mediterranean Sea, for climate change mitigation may be severely compromised if the overall observed trend towards ecosystem loss is not halted. Provided an annual emission in the Mediterranean region of 3.3 tons CO_2 *per capita* (Boisgibault and Mozas, 2012) and a population of about 180 million people (Benoit and Comeau, 2005), the loss of 12 Tg CO_2 of annual carbon sink capacity of *P. oceanica* meadows represents 2% of the total emissions by Mediterranean countries. This is, however, a conservative estimate, as the loss of *P. oceanica* vegetation may potentially trigger CO_2 emissions from the erosion of the thick organic carbon deposits accumulated over millenia in the sediment once the vegetation is lost (Fourqurean et al., 2012; Lo Iacono et al., 2008; Mateo et al., 1997). Conservation measures effective in reducing the current loss rate and possibly recovering some of the area lost would, therefore, contribute to climate change mitigation (Duarte et al., 2013).

Moreover, the reduction by 50% over the last 20 years of the density or biomass of *P. oceanica* observed in the Mediterranean implies a proportional reduction of all those components of their ecosystem functions that may scale to biomass or density, such as dissipation of wave energy (Jeudy De Grissac, 1984), particle and sediment retention and accretion (Jeudy de Grissac, 1984), and productivity (Romero, 2004), Therefore, the provision of services by *P. oceanica*, for instance, increasing water quality, coastal protection, adaptation to sea level rise (Barbier et al., 2011) and buffering coastal acidification (Hendriks et al., 2013) may have already decreased by 50%.

In summary, our results demonstrate an overall tendency towards decline of the areal extent, cover and shoot density of *P. oceanica* meadows since the second half of 20th Century. Available estimates indicate that between 13% and 38% of seagrass areal extent of *P. oceanica* in the Mediterranean basin could have been already lost, and that seagrass cover and shoot density in the remaining areas across the Mediterranean has been thinning. The loss of *P. oceanica* meadows in the Mediterranean may have lead to a similar reduction of the capacity of this key coastal ecosystem to sequester carbon since the second half of 20th Century, and hence that of the entire Mediterranean Sea. Similarly the magnitude of those ecosystem services scaled to *P. oceanica* abundance may have been reduced. The major causes of *P. oceanica* loss have been widespread disturbances acting at local scale, but recently, global disturbances, such are climate change and spreading of invasive exotic species, are also seriously threatening *P. oceanica* meadows in the Mediterranean. These findings urgently call for implementation of management and conservation measures aiming at mitigating coastal deterioration by combining local and global actions, as well as the development of effective technologies for *P. oceanica* revegetation.

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