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Climate change and Mediterranean seagrass meadows: a synopsis for environmental managers

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Abstract

This synopsis focuses on the effects of climate change on Mediterranean seagrasses, and associated communities, and on the contribution of the main species, Posidonia oceanica, to the mitigation of climate change effects through sequestering carbon dioxide. Whilst the regression of seagrass meadows is well documented, generally linked to anthropogenic pressures, global warming could be a cause of new significant regression, notably linked to the introduction of exotic species, the rise of Sea-Surface Temperature (SST), and relative sea level. Seagrass communities could also be affected by climate change through the replacement of high structural complexity seagrass species by species of lower complexity and even by opportunistic introduced species. Although it is currently very difficult to predict the consequences of these alterations and their cascade effects, two main potential conflicting trends in the functioning of seagrass ecosystems are acceleration of the herbivore pathway or the detritivore pathway. The mean net primary production of the dominant species, Posidonia oceanica, is relatively high and can be estimated to range between 92.5 to 273 kg C m⁻² a⁻¹. Around 27% of the total carbon fixed by this species enters the sedimentary pathway leading to formation, over millennia, of highly organic deposits, rich in refractory carbon. At the Mediterranean scale, the sequestration rate might reach 1.09 Tg C a⁻¹. The amount of this stored carbon is estimated to range from 71 to 273 kg C m⁻². When considered at the Mediterranean scale would represent 11 to 42% of the CO₂ emissions produced by Mediterranean countries since the beginning of the Industrial Revolution. The greatest value of the P. oceanica ecosystem, in the context of mitigation of global climate change, is linked to this vast long-term carbon stock accumulated over millennia, and therefore, efforts should be focused on preserving the meadows to keep this reservoir intact.

Keywords: Seagrass ecosystem, Posidonia oceanica, global change, primary production, carbon sink, Mediterranean, seagrasses.

Introduction

Seagrass meadows constitute a major component of coastal marine ecosystems, which provide goods and services to the growing human populations in coastal areas. However, seagrass meadows are presently experiencing a decline globally (Orth et al., 2006); a loss rate of 7% a⁻¹ since 1990 has been computed, which places seagrass meadows among the most threatened ecosystems on earth (Waycott et al., 2009). Worldwide, seagrasses are subjected to all five of the most serious threats to marine biodiversity (Norse, 1993): overexploitation, physical modification, nutrient and sediment pollution, introduction of non-native species, and climate change. Threats to seagrass meadows from climate change include increases in sea surface temperature, sea level, and frequency and intensity of storms (Short & Neckles, 1999), which are predicted to have deleterious effects on seagrasses and represent a pressing challenge for coastal management (Brouns, 1994).
While climate and other global impacts require international actions, regional management practices may help reducing local impacts. Managing seagrass meadows requires efforts to reduce nutrient and organic inputs from agricultural, aquaculture and urban sources, to prevent sediment loading, and to avoid mechanical damage through anchors, trawling and fishing gears (Borum et al., 2004). Best coastal management practices may promote favourable growing conditions to confer seagrass meadows with resistance and resilience against pressures that cannot be managed locally, such as those associated with climate change.

All the above are particularly true for the Mediterranean, a semi-enclosed basin experiencing heavy demographic, urban and industrial pressures (Bianchi & Morri, 2000), and where climate change is showing large impacts (Bianchi & Morri, 2003, 2004). The Mediterranean Sea is considered as a ‘biodiversity hotspot’ (Bianchi and Morri, 2000; Myers et al., 2000) and a ‘miniature ocean’ by physical oceanographers (Béthoux & Gentili, 1999) that can act as a model of the global ocean (Lejeusne et al., 2010). The Mediterranean Sea is a bio-geographical crossroads between the Atlantic and Indo-Pacific Oceans. Its eventful history and the diversity of its environmental conditions explain its high levels of biodiversity (4 to 18% of known marine species, Bianchi & Morri, 2000; Coll et al., 2010) and endemism (almost 25% of the species present; Fig. 1). Geological events at the end of the Miocene Epoch (Messinian crisis) and climate changes in the Pleistocene Epoch (alternation of glacial and interglacial periods) have played a decisive role in the settlement of the present biota (Orfanidis & Breeman, 1999). Mediterranean biodiversity is currently weakened by anthropogenic pressures, introduced species and climate change. These pressures are now proportionately greater than any other sea and ocean (Lejeusne et al., 2010). In addition to the high intensity of these pressures, it is the speed at which they are appearing that is of particular concern.

The Regional Climate Change Index (RCCI; Giorgi, 2006) and several other climate models show, for the Mediterranean Sea, a significant reduction in precipitation, rising temperatures and extreme weather events, which may well lead to aridification, especially in the southern part of the Basin (Elguindi et al., 2011). At shallow depths, two types of climate-driven effects have been observed: a warming trend and an increase in the frequency of exceptional events. A 30-year data set (1974–2005) from the Spanish Catalan coast first demonstrated warming of the littoral at four different depth zones from the sea surface down to 80 m (Salat & Pascual, 2002; Vargas-Yanez et al., 2008; Coma et al., 2009). These data show a clear trend at all depths, with a remarkable warming of 1.4 °C at -20 m. Other data sets (same period, other parts of the NW basin and the Aegean Sea show similar trends (warming by +0.8 to +1.0 °C) over the last 30 years (Prieur, 2002; Rixen et al., 2005; Theocharis, 2008). Satellite observations from 1985–2006 confirm this trend in sea surface temperature with an increase of 0.03 ± 0.008°C yr⁻¹ for the western basin and 0.05 ± 0.009°C yr⁻¹ for the eastern basin (Nykjaer, 2009).

Five species of strictly marine seagrasses (Magnoliophyta) thrive in the Mediterranean and reflect the history and characteristics of this sea:

![Fig. 1: Origins of species dwelling in the Mediterranean Sea (from Boudouresque, 2004, redrawn).](image)
- *Posidonia oceanica* (Linnaeus) Delile, a Mediterranean endemic species that forms vast meadows, from the sea-surface down to 40 m depth in the clearest waters, found in the whole Mediterranean Basin with the exception of the extreme south east. *P. oceanica* plays an important role at the ecological, sedimentary and economic level; it is also a tool used to assess the overall quality of the water and plays a major role in carbon fixation and storage – “blue carbon” (Pergent et al., 1994; Mateo et al., 1997; García & Duarte, 2001; Duarte et al., 2005; Lo Iacono et al., 2008; Nellermann et al., 2009; Serrano et al., 2012).

- *Cymodocea nodosa* (Ucria) Ascherson, a warm affinity species found all over the Mediterranean (particularly in the Eastern Basin), in the Sea of Marmara and in the Atlantic Ocean. In terms of occupied surface area, *C. nodosa* ranks second, after *P. oceanica*, in the Mediterranean Sea.

- *Zostera marina* Linnaeus, a cold affinity species that is widely distributed from north-temperate regions of the Atlantic and Pacific Oceans to the Arctic Circle (Green & Short, 2003). In the Mediterranean, *Z. marina* mainly occurs in coastal lagoons and in the innermost parts of very sheltered bays. At present, this species seems to have disappeared from numerous sites where it was present several decades ago (Fig. 2) and, in localities where *Z. marina* is still present, significant regression has already been recorded (Boudouresque et al., 2009).

- *Zostera noltei* Hornemann, a species most often occurring on intertidal soft substrates in the Atlantic Ocean. In the Mediterranean, *Z. noltei* forms only subtidal meadows in coastal lagoons, the innermost part of some sheltered bays and small harbours. In terms of dynamics, this species demonstrates high resilience, even though several examples of drastic regression have been related to changes in salinity or nutrient enrichment (Ben Maiz & Shili, 2007; Bernard et al., 2007). However, the few cases of regression recorded do not represent a general trend and *Z. noltei* is a species that may benefit from the regression of other seagrasses in the Mediterranean Sea (Boudouresque et al., 2009).

- *Halophila stipulacea* (Forsskål) Ascherson, a tropical species (Indian Ocean, Persian Gulf and Red Sea) which entered the Mediterranean Sea a few years after the opening of the Suez Canal (hence Lessepsian migrant; Den Hartog, 1970). *H. stipulacea* was first reported from Rhodes in 1894 (Fritsch, 1895). Since then it has spread, usually following the prevailing currents (Galil, 2006), and colonized a large part of the Eastern Basin, where it can form vast meadows from the sea-surface down to a depth of 40 m. This species is most often found in shallower habitats (2 to 10 m deep), in sheltered areas and within or near harbours (Gambi et al., 2008).

Here, we will focus on (i) the effects of climate change on Mediterranean seagrasses and on the associated communities (impact and resilience), (ii) the contribution of the main species, *P. oceanica*, to climate change mitigation through its role as carbon sink (fixation and sequestration of Blue Carbon) and (iii) the implications for coastal management practices.

**Decline of Mediterranean seagrass meadows**

The regression of seagrass meadows is a worldwide phenomenon observed over several decades, though the
amplitude of this regression varies depending on the species and geographical zones under consideration (Short & Wyllie-Echeverria, 2000). The five Mediterranean seagrasses are subject to natural and anthropogenic pressures and even if the decline of meadows seems, in general, to be relatively limited (between 0 and 10 % throughout the 20th century; Gonzalez-Correa et al., 2007; Boudouresque et al., 2009), more significant rates of decline (up to 5-8 % per year) were locally observed in places that are subjected to strong anthropogenic pressures (Marbà et al., 1996) while meadows growing in pristine sites remain stable (Bonacorsi et al., 2013). Along the highly urbanised coasts of Liguria, Italy, extensive coastal development during the 1960s led to an estimated 30 % regression of P. oceanica meadows (Bianchi & Peirano, 1995; Peirano & Bianchi, 1997).

The main regressions of Mediterranean seagrass meadows are related to coastal development, exploitation of living resources (aquaculture and fisheries, including trawling), discharge of solid and liquid wastes and the development of pleasure boating and tourism (see synthesis in Boudouresque et al., 2009). However, new pressures, indirectly or directly linked to global change, could be at the origin of significant regressions, notably the introduction of exotic species, and the rise of Sea-Surface Temperature (SST) and sea level (Short & Neckles, 1999; Bouresque & Verlaque, 2002; Marbà & Duarte, 2010).

The recent introduction into the Mediterranean of exotic invasive macrophytes, able to enter into competition with native seagrasses, is a major concern (Boudouresque et al., 2009). For instance, the impact of Caulerpa taxifolia (M. Vahl) C. Agardh and Caulerpa racemosa var. cylindracea (Sonder) Verlaque et al. (Chlorobiobionta) on C. nodosa, P. oceanica and Z. noltei meadows is characterized by (i) a decline in the density of leaf shoots, (ii) an increase in the energy budget dedicated to sexual reproduction (iii) an increase in the synthesis of defence phenolic compounds, which constitutes a classic response to stress (Ceccherelli & Cinelli, 1997; Ceccherelli & Campo, 2002; Pergent et al., 2008) and (iv) a deterioration of sediment quality (Holmer et al., 2009). In addition, even if the capacity of these Caulerpa spp. to eliminate a healthy P. oceanica meadow has yet to be demonstrated, in the short-term, stressed and degraded meadows constitute a very favourable environment for the development of these invasive species, and this development could in turn exacerbate the regression of seagrass meadows (Villéle & Verlaque, 1995; Holmer et al., 2009; Montefalcone et al., 2010a; Kiparissis et al., 2011).

Water temperature constitutes a determinant factor with regard to the distribution of seagrasses (Short et al., 2001) and their distribution in the Mediterranean will shift as a result of increased temperature stress. The absence of P. oceanica in the extreme south east of the basin seems to be directly related to excessively high SST in summer. For instance, at the southern Turkish limit of P. oceanica, a recent decline of meadows has been attributed to the rise in SST (Celebi et al., 2006). In addition to the steady increase in water temperature (Salat & Pascual, 2002; Coma et al., 2009), the positive climatic anomalies recorded in the summers of 1999, 2003 and 2006 have been responsible for a decline in the vitality of P. oceanica (Mayot et al., 2005; Marbà & Duarte, 2010). Declining P. oceanica health, involving growth and sexual reproduction in response to water temperature increase, has been observed in “Stagnone di Marsala” (Tomassello et al., 2009; Calvo et al., 2010), a semi-enclosed coastal lagoon along the western coasts of Sicily (Italy), where seagrass forms reef, atoll and tiger meadow types. The main regression has occurred in the inner part of the lagoon (La Loggia et al., 2004), especially in the last decade when a large part of the seagrass meadow died (SC-AT, personal obs.).

During the “Little Ice Age” (extending from the 13th century to the beginning of the 19th century), cold affinity species, such as Z. marina, may have spread to a significant degree. If global warming intensifies Z. marina is likely to regress in the Mediterranean Sea, or even disappear from its northern Mediterranean refugia. Similarly, the rapid warming observed since the middle of the 19th century may have contributed to the regression of P. oceanica (Peirano et al., 2005; Fig. 2). Zostera noltei forms vast meadows that are subject to wide variations of light intensity and temperature, so the warming trend may not have a significant impact on this species. Conversely, Z. noltei could benefit from the decline of other seagrasses (Haritidas et al., 1990). In general, warm affinity species C. nodosa and H. stipulacea seem to benefit from the warming trend (Boudouresque et al., 2009). Over the past few years, C. nodosa has taken advantage of P. oceanica regression to colonize new areas (Montefalcone et al., 2007). In the same way, the spread of H. stipulacea seems to have accelerated, with colonization of sectors formerly considered as hardly compatible with the development of this tropical species (Gambi et al., 2008).

The rise in sea level observed since the late 20th century may also explain certain recent regressions recorded at the lower distribution limit of P. oceanica meadows. When the limit is situated at the depth of light compensation and on a gently sloping substrate, any rise in sea level, even of a few centimetres, is inevitably accompanied by a linear regression of this limit that may amount to several metres. This adjustment of the plant to its new depth of compensation may be fairly rapid whereas the rise of its upper limit may be insignificant on steeper and more rugged bottoms (Duarte, 2002; Boudouresque et al., 2009; Bonhomme et al., 2010). The rise in sea level will probably continue and may accelerate (IPCC, 2007; Rahmstorf, 2007), resulting in a general upward withdrawal of P. oceanica meadows living close to the depth distribution limit. In addition, a rise in sea level will increase seawater intrusion into estuaries and coastal lagoons (Short & Neckles, 1999).

In the Mediterranean, the average volume of rainfall should decline, but in contrast, the frequency of extreme
rainfall events will probably increase (Christensen & Christensen, 2004; Sánchez et al., 2004; IPCC, 2007). For the species living in shallow water or in relatively enclosed environments (lagoons, bays), this alteration of the rainfall regime should lead to significant changes in the seagrass meadows, according to the ecological characteristics of the species involved. On the one hand, the progression of *C. nodosa*, reported by Barsanti et al. (2007) in one sector of the Gulf of Tigullio (Liguria, Italy), may be a consequence of this phenomenon. On the other hand, severe run-off during extreme rainfall events may negatively affect seagrass meadows causing sediment erosion or burial. Also, the expected alteration of the marine climate regime will imply changed coastal hydrodynamics, especially in term of intensity and frequency of wave action, with dramatic consequences for the positions of both the upper and lower limits of *P. oceanica* meadows (Vacchi et al., 2012).

**Impact of climate change on communities associated with seagrasses**

The five Mediterranean seagrasses provide associated communities with different habitat types, depending on plant morphology and bed architecture. Three levels of structural complexity can be distinguished among the meadows. The lowest level of complexity is found in *H. stipulacea* meadows. *Cymodocea* *nodosa* and *Zostera* spp. meadows show comparatively high structural complexity, while *P. oceanica* meadows show the highest structural complexity and habitat diversity.

When environmental conditions become unfavourable for a species, it may be replaced by another. While *P. oceanica* constitutes the “climax” ecosystem over a large part of Mediterranean shallow water coastal areas, *C. nodosa* and, to a lesser extent, *Z. noltei* can constitute pioneer species in the succession, allowing for the settlement of *P. oceanica* meadows (Boudouresque et al., 2012). However, while *P. oceanica* can be replaced by native species, it can also be replaced by opportunist introduced species (Montefalcone et al., 2010b). This substitution of species by ones having lower structuring capacities may trigger profound changes within the associated communities. However, a possible increase of the thermal optima of species due to an increase in partial pressure of CO$_2$ (pCO$_2$), a phenomenon documented in terrestrial C3 species, may compensate for this trend and increase the resistance of *Posidonia* (C3 species) to the threat of *Cymodocea* (C4 species) threat (Koch et al., 2013). The SST rise is likely to lead to the replacement of *Z. marina* by “warm” affinity species of lower structural complexity, such as *C. nodosa*, *H. stipulacea*, or macrophyte invasive species such as *Caulerpa* spp. and *Womersleyella* *setacea* (Hollenberg) R.E. Norris. The decrease in structural complexity will be even more marked in sectors where *P. oceanica* runs a risk of collapse (e.g. the southern-eastern limit).

Furthermore, the rise in SST, which affects Mediterranean fisheries directly (Tzanatos et al., 2014), may cause two types of alteration in seagrass communities:

- A modification of the relative abundance of closely related species, benefiting those having affinities for the southern parts of the Mediterranean. Thus, at the level of the ichthyofauna in the western Mediterranean, *Serranus scriba* (Linnaeus, 1758) has become more abundant than *S. cabrilla* (Linnaeus, 1758) in recent years, while *Symphodus cinereus* (Bonnetterre, 1788) has declined in abundance in favour of *S. ocellatus* (Forsskål, 1775) (Moranta et al., 2006; Harmelin-Vivien et al., unpublished). A northward displacement of tropical fishes in relation to a rise in SST was also reported from Atlantic seagrass meadows (Gulf of Mexico; Bodri et al., 2010).

- The acclimatization and spread of alien species, particularly those entering the Mediterranean through the Suez Canal (Lessepsian migrants). More than 500 Lessepsian migrants are present in the Mediterranean and a number of them are considered as invasive (Por, 1990; Boudouresque & Verlaque, 2002; Zenetos et al., 2008). The fish fauna of the seagrasses of the Eastern Basin now include several Red Sea species, in particular the herbivores *Siganus liridus* (Rüppell, 1829) and *S. rivulatus* Forsskål & Niebuhr, 1775, consumers of benthic invertebrates such as *Pteragogus pelycus* Randall, 1981, *Stephanolepis diaspros* Fraser-Brunner, 1940, *Upeneus pori* Ben-Tuvia & Golani, 1989 and *Lagocephalus sceleratus* (Gmelin, 1789), and the piscivores *Fistularia commersonii* Rüppell, 1838 and *Sphyraena chrysotaenia* Klunzinger, 1884 (Kalogirou et al., 2010). For a long time after the opening of the Suez Canal, migrant species remained confined to the Eastern Basin. However, this is no longer the case today; for the past fifteen years or so, we have witnessed considerable acceleration of the colonization process in the Mediterranean (Lejeune et al., 2010; Zenetos et al., 2012). The number of new arrivals is constantly on the increase and reports on Lessepsian species in the Western Basin are increasingly frequent. For example, the first observations of *S. luridus* and *F. commersonii* on the French coasts were in 1989 and 1990, respectively (Daniel et al., 2009; Bodilis et al., 2011). This acceleration, which seems to be definitely correlated with the warming of the Mediterranean, is likely to continue in the coming decades (Raitsos et al., 2010).

While modification of the relative abundance of closely related species should not cause any major changes in the functioning of seagrass ecosystems, there is a risk that a massive arrival of invasive alien species may significantly alter their functioning (Boudouresque et al., 2005). For instance, introduced herbivorous fishes (e.g. *Siganidae*) may compete with Mediterranean species such as *Sarpa salpa* (Linnaeus, 1758) and *Sparisoma cretense* (L., 1758) and strongly increase the herbivore pressure, resulting in barren grounds (Harmelin-Vivien et al., 2005; Azzurro et al., 2007; Sala et al., 2011). In addition, certain Lessepsian predators currently in full
expansion phase in the Mediterranean, such as *F. com-mersonii* (Bariche et al., 2009), might increase the predation pressure.

It is currently very difficult to predict with any exactitude the impact of these alterations and their "cascade effects" on the functioning of seagrass ecosystems. However, two main conflicting trends in ecosystem functioning could occur, depending on the sectors considered (Boudouresque et al., 2005):

- Increased grazing pressure, due to Lessepsian migrants (e.g. *Siganus* spp.) and warm affinity species (e.g. *S. cretense*), could accentuate the "herbivore pathway" at the expense of the "detritivore pathway", in the functioning of seagrass ecosystems;

- The rising abundance of primary producers with strong chemical anti-herbivore defences (e.g. *Caulerpa* spp. and *Womersleyella setacea*) could conversely accentuate the dominance of the detritivore pathway (Boudouresque et al., 2005).

Likewise, consequences arising from alterations of the "invertebrate" compartment, strongly influenced by the introduction of new species, climate change, water acidification and the rise in sea level, must also be taken into consideration. We have a spectacular example in the case of the invasive Lessepsian Foraminifera *Amphistegina lobifera* Larsen, 1976, responsible for a high rate of production of biogenic sand and a radical change in habitats in the Eastern Basin (up to 310,000 living individuals per m², and up to 80 cm of test accumulation (Yokeş et al., 2007). Currently occurring in Tunisia and Malta, this species is likely to colonize the Western Basin (Yokeş et al., 2007). Faced with such sedimentary alteration, the fast growing *C. nodosa*, *H. stipulacea* and *Z. noltei* should adapt well, or even be favoured; in contrast, *P. oceanica* will be incapable of tolerating such a high sedimentation rate (Boudouresque & Jeudy de Grissac, 1983).

The global acidification of the oceans may also have an impact on the species, as demonstrated for Mediterranean marine habitats exposed to volcanic CO₂ emissions (pH as low as 6.57) where calcified organisms and populations have been profoundly altered, as has the recruiting of invertebrates (Hall-Spencer & Rodolfo-Metalpa, 2008; Cigliano et al., 2010; Bellissimo et al., 2013). A shift from dominant corallines to fleshy macroalgs in seagrass meadows may reduce light availability in the benthos thus accelerating the regeneration of seagrasses, without taking into account benefits due to their own enhanced photosynthesis (Harley et al., 2012; Koch et al., 2013). On the contrary, such photosynthetic enhancement may increase the pH of shallow bays and coastal lagoons dominated by dense seagrass meadows facilitating calcification (Semesi et al., 2009).

**Contribution to mitigation of the consequences of climate change**

In the Mediterranean Sea, the origin of extreme natural events is either linked to climate (storms and hurricanes - medicanes), or geological occurrences (submarine earthquakes, large-scale landslides or volcanic activity, that generate tsunamis). Although these phenomena are rare, the basin’s recent history confirms that they should certainly not be excluded (Pareschi et al., 2006), especially as certain extreme climatic phenomena seem to be increasingly frequent (Romero et al., 2007). While mangroves, salt marshes, coastal dunes and coral reefs are well known for the role they play in breaking waves and reducing the speed of currents, several seagrass species are also capable of reducing the energy of waves and currents (Koch et al., 2009).

Among their many functions, *P. oceanica* meadows play an important role in stabilizing the seabed, attenuating swells and waves, and enhancing the deposition of sedimentary particles (Sánchez-González et al., 2011; Boudouresque et al., 2012; Infantes et al., 2012). Furthermore, a particular feature common to Mediterranean sandy coastlines is the massive shedding of *P. oceanica* leaves in autumn. The floating dead leaves that are eventually cast ashore also attenuate swells and waves. Finally, dead leaves and other debris of *P. oceanica* build up on the beaches in dense deposits. When conditions allow, this accumulated material can consolidate and produce a very compact and resistant structure, called "banquettes", 95% of which consists of dead leaves (Mateo et al., 2002; Boudouresque et al., 2012). These "banquettes", up to 2 m high and 20 m wide, can stay in place for several years, providing very effective protection against coastal erosion. The replacement of a high biomass species such as *P. oceanica* by smaller species (*C. nodosa* and *H. stipulacea*) could thus reduce beach protection capacity, especially in cases of extreme events.

Several studies highlight the major role played by coastal vegetation (salt marshes, mangroves and seagrasses) in carbon sequestration (Blue Carbon). Seagrasses play a major role as they are estimated to account for 40% of the carbon stored each year by coastal vegetation (Nellemann et al., 2009). Recent estimates by Fourqurean et al. (2012) indicate that, globally, seagrass ecosystems store between 4.2 and 8.4 Pg carbon per year, with a potential maximum of 19.9 Pg organic carbon. The present rates of seagrass loss could therefore result in the loss of their carbon sequestration capacity and the release of up to 299 Tg carbon per year due to soil erosion. Thanks to the unique formation of its thick matte, which may persist for millennia, *P. oceanica* has the largest documented organic carbon stores and can be considered an "outlier" within seagrass species (Fourqurean et al., 2012; Serrano et al., 2012; Lavery et al., 2013). The loss of *P. oceanica* meadows may result in the erosion and rapid remineralization of the carbon-rich soils stored beneath the canopy, in particular in exposed locations, thus releasing CO₂ and accelerating climate change effects.
tion (NPP) (39 to 565 g C m\(^{-2}\) a\(^{-1}\); Pergent-Martini \textit{et al.}, 1994; Fig. 3). For the integrative depth of 15 m, corresponding to the average between the upper and the lower limits of its bathymetric distribution (UNEP-MAP-RAC/SPA, 2009), the mean production could be estimated to be 92.5 < 115.7 < 144.7 g C m\(^{-2}\) a\(^{-1}\) (confidence level = 95%; Fig. 3).

The proportion of this NPP buried in the matte (soil beneath a \textit{P. oceanica} meadow composed of rhizomes, roots and sheaths together with the sediment filling the interstices) is estimated on average to be 30% of the NPP (Pergent \textit{et al.}, 1994, 1997). It is usually possible to distinguish (i) a short-term organic carbon sink (mineralization occurring between 2 and 6 years after burial) and (ii) a long-term sink (a few decades to at least several millennia) (Serrano \textit{et al.}, 2012). The proportion of carbon that joins the sink over the long term (sequestration) is estimated on average to be 27% of the total carbon fixed by the plant (Serrano \textit{et al.}, 2012), which is consistent with the production buried in sediment estimated by lepidochronology studies (Pergent \textit{et al.}, 1997). Taking into consideration the area occupied by \textit{P. oceanica} in the Mediterranean (35 000 km\(^2\) in Pasqualini \textit{et al.}, 1998) and the mean production at 15 m depth, the sequestration might reach up to 1.09 Tg C a\(^{-1}\). Global estimates of the annual carbon sequestration by seagrass meadows vary considerably and range from 80 Tg C a\(^{-1}\) for a surface area of 600 000 km\(^2\) (Duarte & Cebrián, 1996; including the detritus that accumulates on the sediment surface) to 27.4 Tg C a\(^{-1}\) for a re-evaluated surface area of 300 000 km\(^2\) (Duarte \textit{et al.}, 2005). Intermediate values of 35.7 Tg C a\(^{-1}\) (300 000 km\(^2\); Duarte \textit{et al.}, 2010) and 27.4-44.0 Tg C a\(^{-1}\) (330 000 km\(^2\); Nellemann \textit{et al.}, 2009) have been also estimated. The recent focus on carbon trading has intensified interest in Blue Carbon but, overall, these values are based on relatively heterogeneous and scarce data and may be overestimated, due to the poor knowledge about short- vs long-term carbon sinks. Also, a recent study showed that there was an 18-fold difference in the organic carbon stocks among different seagrass habitats and species in Australia (Lavery \textit{et al.}, 2013). We conclude that there is an urgent need for more information on the variability in seagrass sequestration capacities and the factors driving carbon storage variability, in order to improve global estimates of Mediterranean seagrass Blue Carbon storage.

At different Mediterranean sites, natural erosive structures and drillings showed a thickness of \textit{P. oceanica} mattes of up to 6 m in height (Boudouresque & Meinesz, 1982; Lo Iacono \textit{et al.}, 2008). Quantities of carbon sequestered in the mattes were estimated to be 71-273 kg C m\(^{-2}\) (Romero \textit{et al.}, 1994; Lo Iacono \textit{et al.}, 2008; Serrano \textit{et al.}, 2012), which is similar to peat lands (ca. 120 kg C m\(^{-2}\); Warner \textit{et al.}, 1993), and 2.5 to 9.6 Tg C at Mediterranean scale. This represents 11 to 42% of CO\(_2\) emissions produced by Mediterranean countries, through the combustion of fossil fuels since the beginning of the industrial revolution (23 Tg C; CDIAC, 2010).

However, the ecosystem formed by \textit{P. oceanica} hosts an important community of calcareous organisms (mainly Rhodobionta and various invertebrates) and calcification mechanisms may provide the atmosphere with a significant source of CO\(_2\) (Smith & Gattuso, 2009). However, little data exist on the deposition of carbonated sediments.
from these organisms (López-Sáez et al., 2009; review in Serrano et al., 2011). While the refractory storage of organic carbon in the matte leads to significant removal of carbon dioxide, the fact that seagrass meadows sustain high amounts of calcifying organisms in shallow waters contributes negatively to the carbon dioxide sequestration capacity of seagrasses. There is an urgent need for more information on the ratio between CO₂ emitted and CO₂ fixed in seagrass meadows. This point should be investigated more fully in the future in order to improve global estimates of Mediterranean seagrass Blue Carbon storage.

**Implications for environment managers**

Seagrass habitats are of paramount importance worldwide. This statement is especially true for the Mediterranean, which harbours four native and one introduced seagrass species. One of these species, P. oceanica, provides outstanding ecosystem services (e.g. carbon sequestration, sediment trapping and stabilization, protection of beaches against erosion, and contribution to the coastal and offshore foodwebs). The ongoing climate change will radically change this state in several ways: (i) The cold affinity Z. marina could first be trapped in the northernmost parts of the Mediterranean, then become extinct, (ii) the decline of the charismatic and endemic P. oceanica, which is the main service provider of the ecosystem, will continue, especially at its lower limit in response to sea level rise and in the eastern basin where SST is predicted to increase, (iii) although the overall surface area of seagrasses can remain unchanged, some species (e.g. C. nodosa and H. stipulacea) taking advantage of the decline of competitors (e.g. Z. marina and P. oceanica), the structural complexity of the habitats is likely to decrease dramatically, with negative ecological and economical consequences, (iv) introduced multicellular photosynthetic species, especially those of temperate and warm affinities, can outcompete and deteriorate seagrass ecosystems, and (v) introduced metazoans such as the Red Sea Siganus spp., can dramatically overgraze seagrass meadows.

In addition, natural monuments such as P. oceanica reefs, atolls, and tiger meadows growing in shallow waters are particularly exposed to temperature increase, especially when they develop in transitional waters where limited water exchange (Mazzola et al., 2010) could amplify their sensitivity to climate change and accelerate their regression. This scenario could be a real problem in terms of P. oceanica natural monument conservation. Therefore, these particular features should receive much more attention in monitoring programs, in order to validate early signs of regression and implement appropriate actions against climate change effects.

The most important value of the P. oceanica ecosystem, in the context of mitigation of global climate change, is linked to the vast long-term carbon stock accumulated over millennia rather than to the annual flux into the sink, even if this value is significant. However, the accumulated stock constitutes a kind of “time-bomb”. In areas where P. oceanica meadows die and the leaf canopy disappears, the underlying matte is no longer protected against erosion. Erosion can be of natural origin, either due to deep bottom currents acting perpendicular to the shore in deep areas, or to waves and swell in shallow high-energy areas (Boudouresque et al., 2012). Erosion can also result from human activities. Trawling removes the upper layer of rhizomes of the dead matte. Anchoring of small leisure boats scars the dead matte. The anchor of large leisure boats, cruise liners and war ships digs deep trenches within the dead matte and removes huge blocks of matte (Ganteaume et al., 2005; Boudouresque et al., 2012; MV, personal obs.). Dismantling of the matte will increase organic matter remineralisation rates due to exposure to oxygen and return the carbon stored during millennia into the environment in the form of carbon dioxide, thus accelerating climate change in a similar way as fossil fuels do, but also trapped contaminants (e.g. Mercury, Pergent & Pergent-Martini, 1999).

Management efforts should therefore be focused on, (i) reducing the decline of P. oceanica, the seagrass whose role in the structural complexity of habitats and the carbon sink is the most prominent, especially in areas where human activities are directly involved in the decline (anchoring, trawling, fish farming, pollution); (ii) keeping the P. oceanica carbon reservoir intact in order to prevent the large accumulated stock from being released to the hydrosphere and the atmosphere. This means that even dead matte areas should be preserved from trawling and anchoring of large boats; (iii) preventing the introduction of non-indigenous species and combating whenever possible the expansion of already established invasive species, and (iv) protecting the refuge habitats of Z. marina in northern Mediterranean areas, especially in coastal lagoons. Managing seagrass meadows to improve resilience and to preserve carbon reservoirs from release seems, therefore, to be the most sensible recommendation (Björk et al., 2008; Pergent et al. 2012).

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