Mediterranean Marine Science

Vol 15, No 2 (2014)

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doi: 10.12681/mms.621

Review Article

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
The journal is available on line at http://www.medit-mar-sc.net
Doi: http://dx.doi.org/10.12681/mms.621

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

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Handling Editor: Argyro Zenetos

Received: 12 September 2013; Accepted: 18 January 2014; Published on line: 28 February 2014

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 144.7 g 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}, which when considered at the Mediterranean scale would represent 11 to 42% of the CO_2 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:

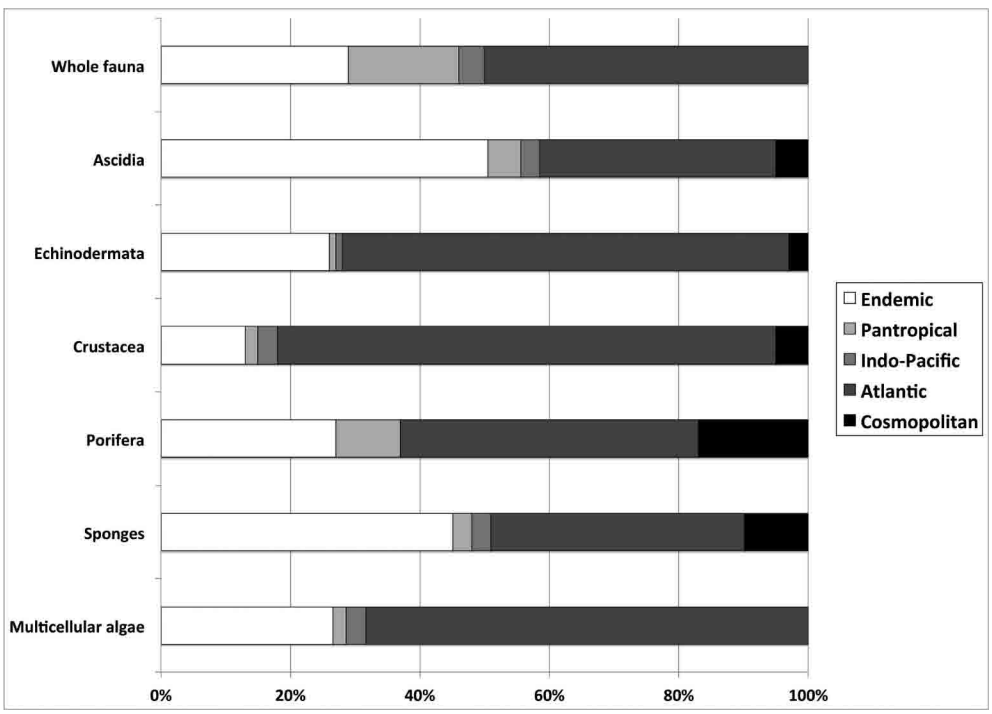

Fig. 1: Origins of species dwelling in the Mediterranean Sea (from Boudouresque, 2004, redrawn).

- *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; Gacia & Duarte, 2001; Duarte *et al*., 2005; Lo Iacono *et al*., 2008; Nellemann *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

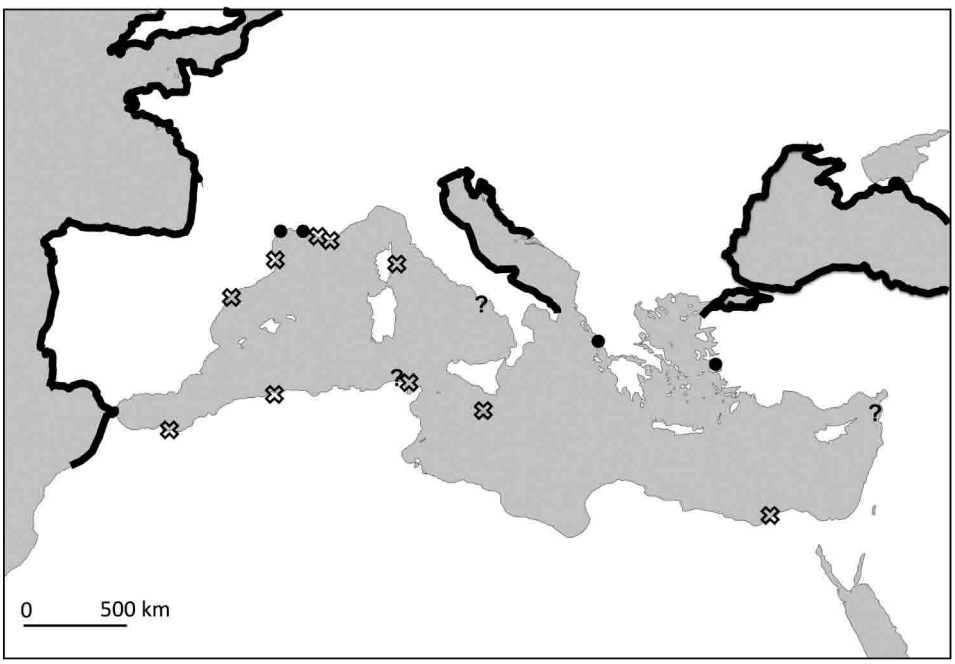

Fig. 2*:* Distribution of *Zostera marina* in the Mediterranean Sea and in adjacent areas (black outline: area where the species is frequently found; black cross: localities where the species has disappeared (bibliographical data); black dots: isolated locations; question marks: presence to be confirmed (old citation). (Base map from Daniel Dalet / d-maps.com).

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; Boudouresque & 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. (Chlorobionta) 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 (Villèle & 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" (Tomasello *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 (Haritonidis *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 opportunistic 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* (Bonnaterre, 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; Fodrie *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 luridus* (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 (Lejeusne *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 2008 and 2009, 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. commersonii* (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 CO_2 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 macroalgae in seagrass meadows may reduce light availability in the benthos thus accelerating the regression 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 (Nelleman *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 remineralisation of the carbon-rich soils stored beneath the canopy, in particular in exposed locations, thus releasing CO_2 and accelerating climate change effects.

Posidonia oceanica has a high Net Primary Produc-

tion (NPP) (39 to 565 g C m^{-2} a^{-1}; Pergent-Martini *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 *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 *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 *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 *et al*., 2012), which is consistent with the production buried in sediment estimated by lepidochronology studies (Pergent *et al*., 1997). Taking into consideration the area occupied by *P. oceanica* in the Mediterranean (35 000 km^2 in Pasqualini *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 km² (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 km² (Duarte *et al*., 2005). Intermediate values of 35.7 Tg C a^{-1} (300 000 km²; Duarte *et al*., 2010) and 27.4-44.0 Tg C a^{-1} (330 000 km²; Nellemann *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 *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 *P. oceanica* mattes of up to 6 m in height (Boudouresque & Meinesz, 1982; Lo Iacono *et al*., 2008). Quantities of carbon sequestered in the mattes were estimated to be 71 - 273 kg C m^{-2} (Romero *et al*., 1994; Lo Iacono *et al*., 2008; Serrano *et al*., 2012), which is similar to peat lands (ca. 120 kg C m^{-2}; Warner *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 *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

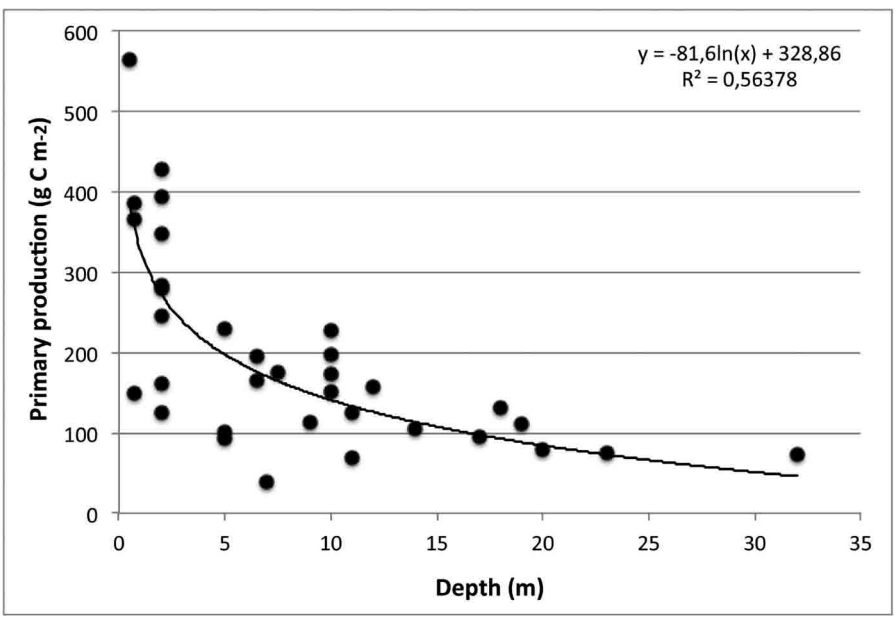

Fig. 3: *Posidonia oceanica* Net Primary Production (blades, sheaths and rhizomes) at several sites in the Mediterranean Sea, as a function of depth (data compiled from Pergent-Martini *et al*., 1994; Pergent *et al*., 1997; Guidetti, 2000; Vela *et al*., 2006; Djellouli, 2007).

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 CO_2 emitted and CO_2 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 valuate 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).

Acknowledgements

The authors would like to thank IUCN-Med for financial support and the reviewers for their useful comments and help in improving this paper.

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