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VULNERABILITY OF AQUATIC ECOSYSTEMS

Review Paper

The necromass of the *Posidonia oceanica* seagrass meadow: fate, role, ecosystem services and vulnerability

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Abstract *Posidonia oceanica* is a seagrass endemic to the Mediterranean Sea. Most of the primary production of the *P. oceanica* meadow is not directly consumed by herbivores and plays a role as dead rhizomes and roots, dead leaves and drift epibionts (hereafter necromass). The fate of this necromass is (i) sequestration within the *matte*, (ii) consumption by detritus-feeders within the meadow, (iii) export towards other marine ecosystems, where it constitutes a source for food webs, (iv) export towards beaches, where it constitutes *banquettes*, reduces the impact of waves and contributes to the beach ecosystem, and (v) export towards the terrestrial dune ecosystem. These five stocks can exchange necromass. The ecosystem services of the *P. oceanica* necromass are pivotal. For example, the role of *P. oceanica banquettes* is fundamental in protecting beaches from erosion, and the carbon sequestration within the *matte* contributes to the mitigation of emissions of CO_2. Human impact on each of these stocks can affect the other stocks and their ecosystem services. The removal of *banquettes* from beaches can have a dramatic negative impact on *P. oceanica* ecosystem services, including the sustaining of beaches. The erosion of *matte* due to trawling and anchoring can remobilize the sequestrated carbon stock.

Keywords *Posidonia oceanica* · Seagrass · Necromass · Detritus-feeders · Beaches · Ecosystem services

Introduction

Posidonia oceanica (Linnaeus) Delile is a seagrass (Magnoliophyta) endemic to the Mediterranean Sea. All records from outside this sea are due to misidentifications (Boudouresque & Verlaque, 2008). Within the Mediterranean, it constitutes extensive meadows throughout virtually the whole of this sea, with the exception of the extreme south-east (from the Nile Delta to south-east Turkey), the northern Adriatic Sea, most of the shores of Languedoc (France) and the vicinity of Gibraltar Straits (Pergent et al., 2012). It dwells from the sea surface down to 20–40 m depth

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(more rarely down to 45 m), depending not only upon water transparency (Molinier & Picard, 1952; Augier & Boudouresque, 1979; Boudouresque & Meinesz, 1982; Orfanidis et al., 2005; Boudouresque et al., 2009; Marbà & Duarte, 2010; Boudouresque et al., 2012; Pergent et al., 2012; Montefalcone et al., 2013), but also upon water movement (Vacchi et al., 2012, 2014).

Rhizomes and leaf shoots can grow horizontally, to colonize the substrate (plagiotropic rhizomes). The leaf canopy traps autochthonous and allochthonous sediment. To resist being buried, rhizomes can also grow vertically (orthotropic rhizomes) (Fig. 1; Molinier & Picard, 1952; Caye, 1980; Boudouresque & Meinesz, 1982; Caye, 1982; Di Maida et al., 2013). Orthotropic rhizome growth ranges from a few millimetres to 77 mm annum^{-1} (Boudouresque et al., 1984). The structure constituted by live and dead parts of rhizomes and roots, together with the sediment which fills the interstices, is called 'matte'. Sediment trapping and orthotropic rhizome growth result in the rising of the *matte* and therefore of the sea bottom over time (Figs. 2, 3); the average rise ranges between 10 and 100 cm per century (Molinier & Picard, 1952; Picard, 1953; Boudouresque & Jeudy de Grissac, 1983; Mateo et al., 1997; Lo Iacono et al., 2008; Rovere et al., 2010; Boudouresque et al., 2012; Serrano et al., 2012).

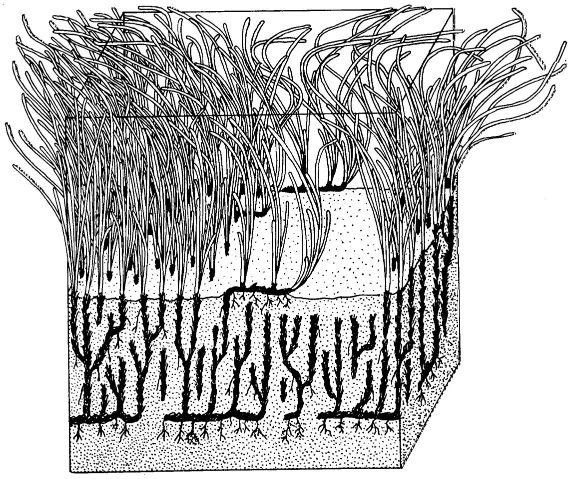

Fig. 1 Horizontal and vertical growth of rhizomes and leaf shoots (plagiotropic and orthotropic growth, respectively) in a *P. oceanica* meadow. From Boudouresque & Meinesz (1982), courtesy of the Port-Cros National Park

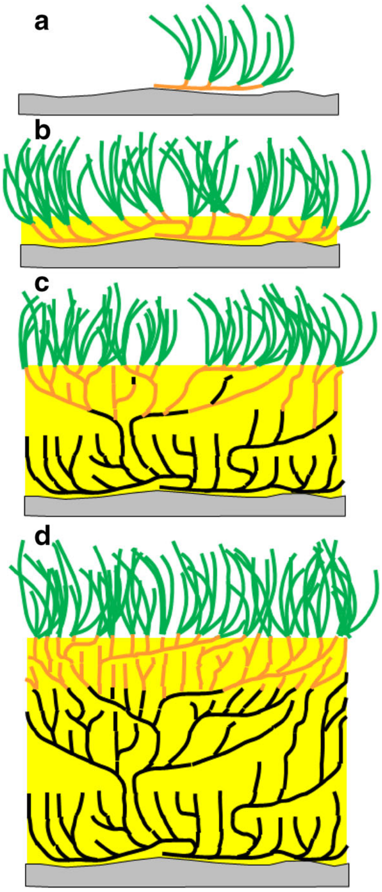

Fig. 2 The rising of the *P. oceanica matte* over time. **a** Arrival of a cutting (or a seed). **b, c, d** Autochthonous and allochthonous sediment is trapped by the leaf canopy. To resist being buried, erect (orthotropic) rhizomes grow vertically, which results in the building up of the *matte*. *Green P. oceanica* leaves. *Brown* living parts of the rhizomes. *Black* dead parts of the rhizomes. *Yellow* sediment. *Grey* initial substrate (sand or reef)

The primary production of the *P. oceanica* ecosystem is of three kinds (Fig. 4): (i) First, the living seagrass itself (leaves, rhizomes and roots), which is usually weakly consumed by herbivores, due to structural and chemical (phenolic compounds) defences (Cariello et al., 1977; Piovetti et al., 1984; Pergent et al., 1994; Agostini et al., 1998; Vergés et al., 2011); (ii) Second, leaf epibionts, mainly cyanobacteria, brown algae (Phaeophyceae) and Rhodobionta, which are highly palatable and are therefore consumed (Vizzini et al., 2002; Tomas et al., 2005; Gacia et al., 2009; Boudouresque & Verlaque, 2013) and (iii) Third, rhizome epibionts, which include poorly palatable Chlorobionta, e.g. *Flabellia petiolata* (Turra) Nizamuddin, calcified Rhodobionta such as *Peyssonnelia* spp. and invasive exotic species such as

Fig. 3 A trench dug into the *matte* shows the actual density of the rhizomes. For the sake of clarity in the drawings (Figs. 1, 2), the density of *P. oceanica* rhizomes within the *matte* has been strongly reduced. Photo © Sandrine Ruitton

Womersleyella setacea (Hollenberg) R.E. Norris, *Lophocladia lallemandii* (Montagne) F. Schmitz, *Acrothamnion preissii* (Sonder) E.M. Wollaston and *Caulerpa cylindracea* Sonder (Boudouresque et al., 2006; Ballesteros et al., 2007; Deudero et al., 2011; Tomas et al., 2011; Boudouresque & Verlaque, 2013). Overall, the net primary production and the biomass of primary producers of the *P. oceanica* ecosystem are conspicuously high; they decrease with depth, paralleling the decrease in irradiance (e.g. Boudouresque et al., 1983; Libes et al., 1983; Mazzella & Ott, 1984; Francour, 1985; Romero-Martinengo, 1985; Pergent et al., 1997; Cebrián & Duarte, 2001; Mateo et al., 2003; Romero, 2004; Gambi et al., 2005; Costantino et al., 2006; Vela et al., 2006; Vergés et al., 2007a, b).

The fate of the primary production

Leaf epibionts can be widely consumed, at least when herbivores such as the sea urchin *Paracentrotus lividus* (Lamarck, 1816), the teleost *Sarpa salpa* (Linnaeus, 1758), crustaceans, such as *Dexamine spinosa* (Montagu, 1813), mainly a diatom-feeder and gastropods, such as *Gibbula umbilicaris* (Linnaeus, 1758), are present (e.g. Nédélec & Verlaque, 1984; Velimirov, 1984a; Gambi et al., 1992; Lepoint et al., 2000; Vizzini et al., 2002; Tomas et al., 2005; Gacia et al., 2009; Boudouresque & Verlaque, 2013). In contrast, *P. oceanica* leaves are generally rarely consumed alone (Verlaque, 1981; Lepoint et al., 2000; Cebrián & Duarte, 2001; Boudouresque et al., 2006). The grazing of leaves has been estimated at 1–13% (mean: 5%) of net primary production (Cebrián & Duarte, 2001); as far as the total primary production of *P. oceanica* (including roots and rhizomes) is concerned, the consumption-assimilation was estimated between 3 and 10% in Provence and Italy, respectively (Pergent et al., 1997), and between 2 and 5% in shallow sites in Tunisia (Djellouli, 2007). However, higher grazing rates have been reported from Marine Protected Areas (MPAs) in Spanish and French Catalonia (Prado et al., 2007; Ferrari et al., 2008), Provence (Laborel-Deguen & Laborel, 1977), eastern Algeria (Pergent et al., 1993) and in several shallow sites (Vela et al., 2006).

Part of the non-consumed *P. oceanica* leaves is shed and accumulates (together with their epibionts) within the litter, where they are the basis of the detritus food web (Fig. 4; Pergent et al., 1994; Mateo & Romero, 1997; Pergent et al., 1997; Boudouresque et al., 2006; Lepoint et al., 2006; Vizzini, 2009; Boudouresque et al., 2012; Costa et al., 2014). The litter also receives inputs from unpalatable epibionts of the rhizomes, broken rhizomes with roots and leaf bundles and drift macrophytes from adjacent sublittoral soft bottom and reef habitats. Here, we call ‘necromass’ the mass of shed primary producers, either shed leaves, broken rhizomes and/or drift macrophytes, together with dead rhizomes and roots within the *matte* (see below). Through its influence on food web composition and dynamics, the necromass often increases the stability and persistence of the ecosystems characterized by its abundance (Moore et al., 2004).

Directly (just after shedding) or indirectly (i.e. after a temporary stay within the litter reservoir), part of the leaf and rhizome necromass is exported out of the *P. oceanica* meadow (Figs. 4, 5). Exported necromass rate ranges between 10 and 55% of the total primary production, depending upon depth, hydrodynamism and region (Pergent et al., 1994, 1997; Mateo et al., 2003). Necromass export has a threefold destination. (i) First, towards beaches. Dead leaves and some broken rhizomes with leaf bundles constitute *banquettes*, which can reach thicknesses of up to 2.5 m (Fig. 5; e.g. Picard, 1965; Boudouresque & Meinesz,

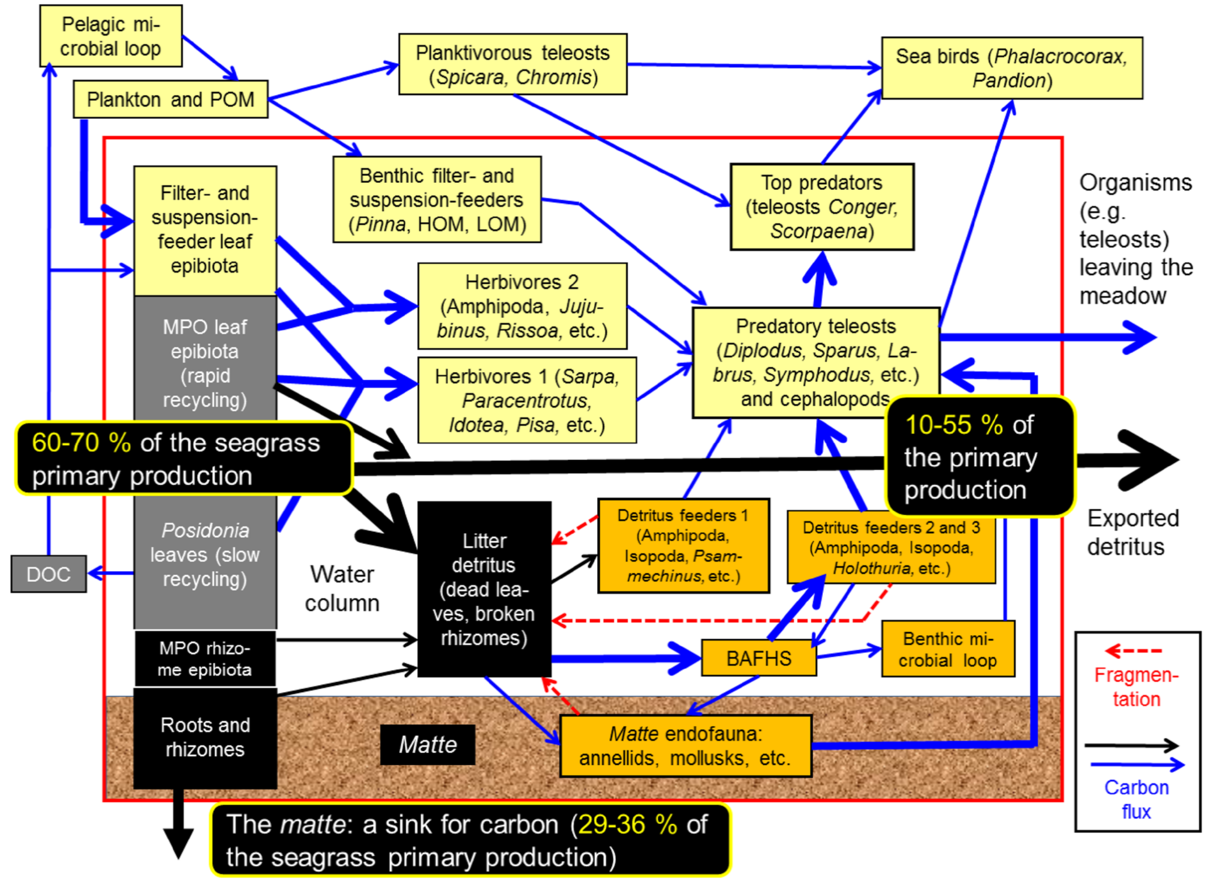

Fig. 4 Conceptual model of the functioning of the *P. oceanica* ecosystem (from Personnic et al., 2014, modified). The width of *solid arrows* (carbon flux) is related to the relative intensity of the flux between compartments, with three levels of intensity. *Black arrows* carbon flux involving necromass; *blue arrows* other carbon flux. *Black and grey boxes* compartments contributing to the necromass, totally or partially, respectively. *Orange boxes* compartments mainly utilizing seagrass necromass as a trophic resource. *Light yellow boxes* other compartments. *BAFHS* bacteria, archaea, fungi and heterotrophic stramenopiles; *DOC* dissolved organic carbon; *HOM* and *LOM* benthic filter- and suspension-feeder indicators of high and low level of organic matter, respectively; *MPO* multicellular photosynthetic organisms other than seagrasses; *POM* particulate organic matter. The proper *P. oceanica* ecosystem is included within the *red rectangle*; *arrows entering the rectangle* correspond to inputs, *arrows going out* are outputs

1982; Farghaly & Denizot, 1984; Jeudy de Grissac & Audoly, 1985; Chessa et al., 2000; Walker et al., 2001; Mateo et al., 2003; Deidun et al., 2011; Boudouresque et al., 2012; Pergent et al., 2012). *Banquettes* experience complex construction and destruction dynamics throughout the year (Gómez-Pujol et al., 2013; Simeone et al., 2013). From the beach, the dead leaves can be blown by the wind up to the dune and foredune, several dozen to several hundred metres inshore (Guala et al., 2006; Cardona & García, 2008). (ii) Second, towards sublittoral reef habitats, where they can be a basis for *Paracentrotus lividus* sea urchin diet (Verlaque & Nédélec, 1983; Verlaque, 1987). Export also concerns sublittoral sandy habitats (Dimech et al., 2006; Cresson et al., 2012), sublittoral dead *matte* habitats (see below) and sublittoral caves (Picard, 1965; Marc Verlaque, unpublished data). (iii) Third, towards deep water, like other seagrasses (Wolff, 1976, 1980; Suchanek et al., 1985). A 'rain' of *P. oceanica* dead leaves and rhizomes falls on circalittoral and bathyal zones, sensu Pérès (1967) (Picard, 1965; Boudouresque et al., 1990; Fourt & Goujard, 2012). Depending upon the weather (calm or stormy), current speed and season, exchanges occur between necromass stocks; *banquettes* move from one part of the beach to another; litter is swept toward deep

Fig. 5 A *banquette* of drift *P. oceanica* leaves and broken rhizomes on Barcaghju beach (Capicorsu, northern Corsica). The figure (Michèle Perret-Boudouresque) gives the scale. Photo © Boudouresque

water or carried toward the beach, while the *banquettes* material can return to the sea (Fig. 6; Mateo et al., 2003; Cantasano, 2011). Overall, *banquettes* do not constitute a significant sink for carbon and nutrients; the only 'lost' (more accurately, transferred) material is constituted by dead leaves consumed by terrestrial detritus-feeders and leaves exported further away to the dunes and foredunes (Mateo et al., 2003; Cardona & García, 2008).

Finally, within the *matte*, rhizomes can be alive down to 30 cm below the bottom surface and the roots down to 70 cm (Francour, 1985). Deeper and older rhizomes and roots are dead and therefore belong to the necromass. Due to phenolic compounds and anoxia, *P. oceanica* remains persist within the *matte* for millennia; the *matte* therefore constitutes a sink for carbon (Molinier & Picard, 1952; Boudouresque et al., 1994; Mateo et al., 1997; Boudouresque et al., 2006; Lo Iacono et al., 2008; Boudouresque et al., 2012; Pergent et al., 2012, 2014). On an average, 29–36% of the primary production (leaf sheaths, rhizomes and roots) is stocked within the *matte* (Pergent et al. 1994, 1997). In the short run, erosion processes, such as 'shifting intermattes' (Boudouresque et al., 1980b, 2012), can transfer to the litter, to the beaches and/or to deep water the surface layer of the *matte* (Figs. 6, 7). In the long run (at the geological scale), the *matte* constitutes a genuine carbon sink that is involved in the diagenesis of hydrocarbons (oil) (Burollet et al., 1979).

A particular case is that of 'dead matte' habitats (Fig. 6). When a *P. oceanica* meadow dies, either naturally or due to human impact, the *matte* may persist for decades and even centuries and can occur over extensive continuous areas or as patches intermixed among living *P. oceanica* meadows (Augier & Boudouresque, 1970; Boudouresque et al., 1980a; Gattorna et al., 2006; Montefalcone et al., 2006, 2007a, b; Boudouresque et al., 2009; Montefalcone

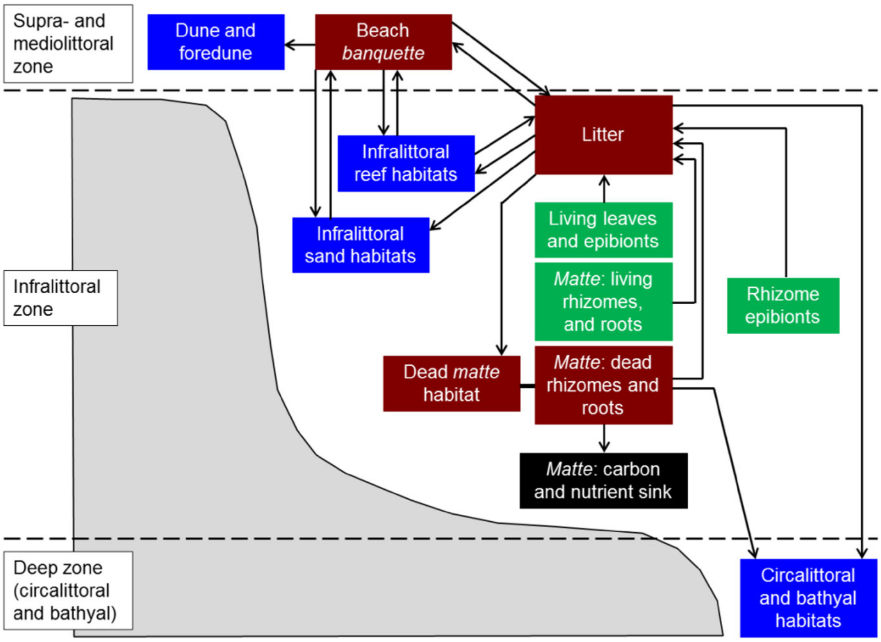

Fig. 6 The fate of the *P. oceanica* seagrass necromass. *Green* living seagrass compartments. *Dark brown* compartments originating in seagrass necromass. *Black* sink. *Blue* other habitats. *Arrows* fluxes of seagrass necromass. Some possible fluxes are not represented, in order to make the sketch clearer. The *line between dead matte habitat* and *matte* means a change over time, not a flux (see text)

Fig. 7 A block of *P. oceanica matte*, ~30 cm wide, washed up after a storm on a beach (Barcaghju, Capicorsu, northern Corsica). Photo © Boudouresque

et al., 2013). The dead *matte*, formed by dead rhizomes and roots and by the sediment filling the interstices, constitutes a peculiar habitat, intermediate between soft and hard bottoms. Sessile species dwell on rhizome tips emerging from the *matte* surface, while the dead *matte* harbours a wide diversity of motile macroinvertebrate species (Harmelin, 1964; Pérès & Picard, 1964; De Metrio et al., 1980; Vaccarella et al., 1981; Borg et al., 2006). Macroinvertebrates are more abundant and more diverse within dead than living matte: ~200–250 versus 100–125 individuals and ~55–80 versus 40–55 species per 25-cm core, respectively (Borg et al., 2006).

Role and ecosystem services

The *P. oceanica* seagrass meadows are involved in a number of ecosystem services (for ecosystem service assessments, see e.g. Costanza et al., 1997; Balmford et al., 2002; Balmford & Bond, 2005; Mulongoy & Gidda, 2008; Pesche et al., 2013; Vassallo et al., 2013) (Fig. 8): (i) A huge Net Primary Production (NPP) (both the seagrass and its epibionts). A small part of the *P. oceanica* NPP is directly used by the herbivores dwelling within the ecosystem, at least in most of the Mediterranean Sea (Mateo & Romero, 1997); in contrast, the leaf-epibiont NPP, which can be quantitatively similar to the seagrass NPP, is widely used by macro- and meso-herbivores (Boudouresque et al., 2012; Personnic et al., 2014). Both NPPs fuel the opulent food web of the ecosystem, including teleost species that are targeted by artisanal fishers (Fig. 8: box 1). (ii) A spawning ground and nursery (Francour & Le Direac'h, 1995; Harmelin-Vivien et al., 1995; Jimenez et al., 1996; Boudouresque et al., 2012) (Fig. 8: box 2). (iii) Export of necromass to adjacent habitats, such as sublittoral reef habitats, sublittoral sandy habitats, sublittoral caves, circalittoral and bathyal habitats (Picard, 1965; Verlaque & Nédélec, 1983; Verlaque, 1987; Dimech et al., 2006; Cresson et al., 2012; Fourt & Goujard, 2012) (Fig. 8: box 3). Directly (within the *P. oceanica* ecosystem) or indirectly (through teleosts leaving the seagrass meadow and exportation of necromass to adjacent habitats), the ecosystem contributes strongly to the landings of Mediterranean commercial fisheries (Jackson et al., 2015). (iv) Sediment stabilization on sublittoral soft bottoms and reduction in turbidity through to reduced particle resuspension (Terrados & Duarte, 2000) (Fig. 8: box 4). (v) Sequestration of carbon within the *matte* (Mateo et al., 1997; Pergent et al., 2012, 2014) (Fig. 8: box 5). (vi) Net production of oxygen linked to carbon sequestration (Bay, 1984) (Fig. 8: box 6). (vii) Reduction in swell and wave strength, resulting in enhanced sand deposition, beach progradation and hence protection of beaches from erosion (Boudouresque & Jeudy de Grissac, 1983; Gacia & Duarte, 2001; Duarte, 2004; Sánchez-González et al., 2011; Stratigaki et al., 2011; Infantes et al., 2012; Manca et al., 2012) (Fig. 8: box 7). (viii) Protection of the beaches from erosion, through the coating of the beaches and the cushioning of the wave impact by the *banquettes* (Fig. 8: box 8). (ix) Stabilization of the dunes and input of nitrogen and organic carbon to the dune and foredune vegetation, by means of dead *P. oceanica* leaves (Fig. 8: box 9). Hereafter, we describe further the ecosystem services (iii), (v), (vi), (viii) and (ix), which are directly or indirectly linked to the *P. oceanica* necromass.

The role of the necromass exported towards adjacent habitats (10–55% of the total NPP; Pergent et al., 1994; Mateo et al., 2003) is obviously pivotal (Fig. 8: box 3). However, there have been very few attempts to assess its role. In sublittoral reef habitats, dead leaves of *P. oceanica* can constitute up to 40% of the gut content of sea urchins (*Paracentrotus lividus*) located hundreds of metres from the nearest meadow (Verlaque & Nédélec 1983; Maggiore et al., 1987; Verlaque, 1987; Boudouresque & Verlaque, 2013). In the Gulf of Calvi (Corsica), *P. oceanica* contributes

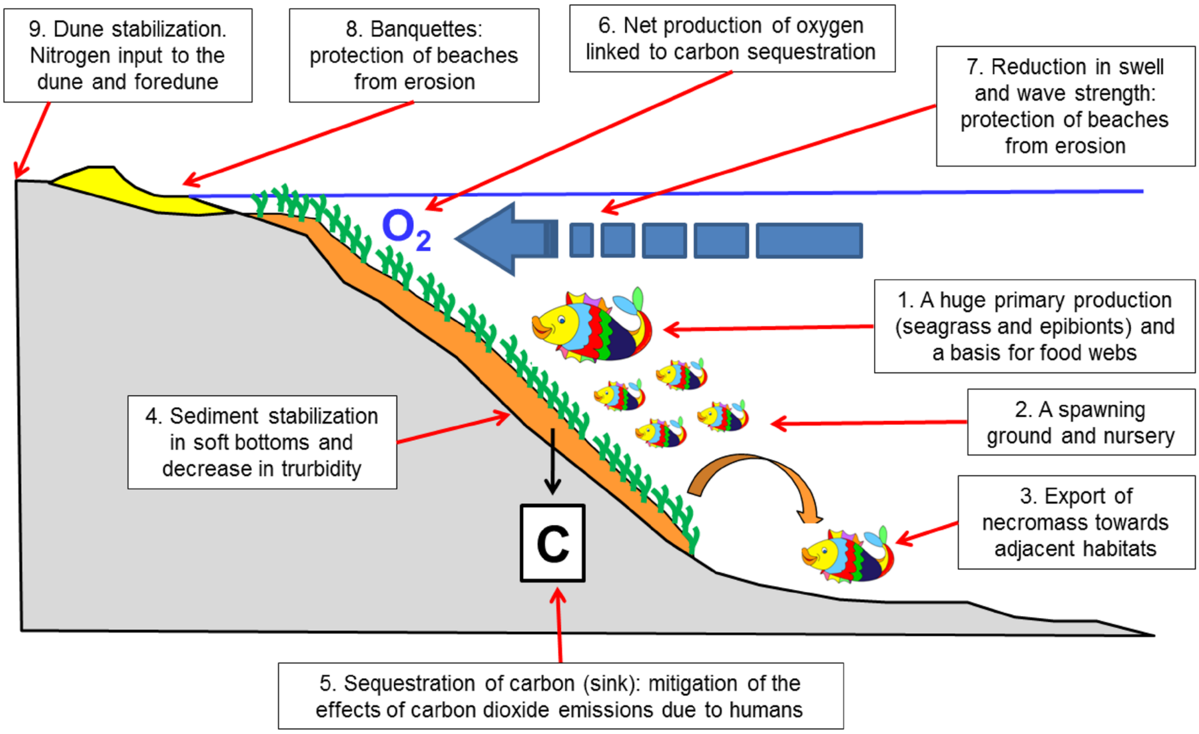

Fig. 8 A summary of the ecosystem services of the *P. oceanica* ecosystem

roughly 12% to the carbon content of such individuals (Dauby, 1989). As far as sandy habitats are concerned, in bays of the Maltese Islands, accumulations of dead *P. oceanica* leaves may cover up to 80% of the bottom in winter and persist until late spring, with small isolated patches (~ 1 m^2) remaining during the summer; a rich fauna of detritivorous crustaceans, mostly amphipods, exploits this necromass (Dimech et al., 2006). Further evidence of the effectiveness of this consumption is provided by means of gut content and stable isotope analyses of the amphipod *Gammarus aequicauda* and isopods of the genera *Idotea* and *Cleantis* (Martynov, 1931), in Corsica (Lepoint et al., 2006; Sturaro et al., 2010). Finally, the dissolved organic carbon (DOC) leached by shed or torn off *P. oceanica* leaves contributes to the DOC stock of the pelagic coastal habitat and to the microbial loop (Velimirov, 1984b).

Sequestration of carbon within the *matte* (carbon sink) is due to the fact that carbon recycling does not occur in deep layers of the *matte* (Fig. 8: box 5). Seagrasses play a major role as they are estimated to account for 40% (50 million metric tons of carbon per year) of the carbon stored each year by coastal vegetation (Nellemann et al., 2009). In *P. oceanica*, the proportion of carbon that joins the sink (sequestration) over the long term is estimated at 10–27% of the total carbon fixed by the plant, which represents up to 9 million metric tons per year at the scale of the Mediterranean (Pergent et al., 2012, 2014). In the Balearic Islands (Spain), it is estimated that the annual carbon sequestration by *P. oceanica* offsets 9% of the islands' total CO_2 annual emissions (MacCord & Mateo, 2010; Pergent et al., 2012).

The net production of oxygen by the *P. oceanica* ecosystem (Fig. 8: box 6) is linked to carbon sequestration. It is worth emphasizing that the mineralization of organic carbon consumes roughly the same quantity of oxygen as that produced by photosynthesis (Cloud & Gibor, 1970; Walker, 1980; Keeling, 1995). The so-called oxygen production by some marine and continental ecosystems (e.g. forests), often highlighted by the media, is therefore a myth, in the absence of long-term (at geological scale) sequestration of carbon. Such long-term sequestration does occur in the *P. oceanica* meadow, which therefore really does produce oxygen.

The *banquettes* of dead *P. oceanica* leaves and rhizomes, on the beaches, contribute to their protection from erosion by swell and waves, particularly during winter storms (Fig. 8, box 8) (Boudouresque & Meinesz, 1982; Roig i Munar & Prieto, 2005; Simeone, 2008; Bovina, 2009; Boudouresque, 2010; Cantasano, 2011; Boudouresque et al., 2012; Pergent et al., 2012; Simeone & De Falco, 2012, 2013). Profiles of a beach, before and after the mechanical elimination of the *banquette*, were made at Mallorca (Balearic Islands); after a stormy episode, the erosion of both the 'cleaned' beach and the foredune was conspicuous (Roig i Munar & Prieto, 2005). In addition, the presence of a thick *banquette* of dead *P. oceanica* leaves on a beach is an excellent biological indicator of the high quality of the marine coastal environment since it marks the presence of extensive healthy *P. oceanica* meadows (Cantasano, 2011). However, according to Gómez-Pujol et al. (2013), the protective role of the *banquettes* should be reconsidered, at least for semi-enclosed sandy beaches where *banquette*s undergo complex construction and destruction dynamics from one month to the next. A rich macrofauna (gastropods, crustaceans, annelids and insects) inhabits the *banquettes*, especially the 'aged' banquettes that have been established for some years; on Maltese beaches, the mean density of the gastropod *Truncatella subcylindrica* (Linnaeus, 1767) was ~6300 individuals m^{-3} (Deidun et al., 2007, 2009). Isotopic analysis established the absence of a direct dietary link between *P. oceanica* detritus and the invertebrate fauna of a sand beach (Colombini et al., 2009; Deidun et al., 2007, 2009); to date, the isotopic signature of the fauna actually inhabiting thick and aged *banquettes* has not been studied. Whatever the role of the *P. oceanica* detritus in the diet of the harboured fauna, *banquettes* are vitally important as a physical structure that provides detritivorous and predatory species with refuge from environmentally stressful conditions (Colombini et al., 2009) and top predators such as sea birds (Bartoli & Prévot, 1978; Bartoli & Holmes, 1997).

Finally, the input of *P. oceanica* leaves to the dune and foredune enhances the formation of the dune and of its colonization by psammophilic vegetation (Bovina, 2009) and constitutes a useful source of nitrogen and organic carbon for the vegetation of the foredune (Cardona & García, 2008) (Fig. 8, box 9).

The economic value of seagrass ecosystems, based upon the ecosystem services, is very high (e.g. Costanza et al., 1997; Waycott et al., 2009). At world scale, for seagrass beds and 'macroalgae' stands, it was estimated at ~19,000 US\$ ha^{-1} $annum^{-1}$ (Costanza et al., 1997); this value was an average for a variety of seagrasses (from the large-sized ecosystem engineers *Posidonia* spp. to less structuring species such as *Halophila* spp.) and macroalgal (from large-sized kelp species to ephemeral turf) habitats, which provide ecosystem services that are probably highly contrasted. This value was higher than that of wetlands (~15,000 US\$ ha^{-1} $annum^{-1}$), mangroves and tidal marsh (~10,000 US\$ ha^{-1} $annum^{-1}$), coral reefs (~6000 US\$ ha^{-1} $annum^{-1}$) and tropical forests (~2000 US\$ ha^{-1} $annum^{-1}$). For the *P. oceanica* meadow, higher values have been proposed (Blasi, 2009; Blasi & Cavalletti, 2010; Rovere et al., 2010; Vassallo et al., 2013; Pergent et al., 2014). A partial assessment, based upon nursery role, sediment retention, reduction of hydrodynamics, shore protection, primary production and water oxygenation, resulted in a value of 172 € m^{-2} $annum^{-1}$ (~1,900,000 US\$ ha^{-1} $annum^{-1}$) (Vassallo et al., 2013).

Vulnerability

Key components of vulnerability are exposure to natural and anthropogenic impact, sensitivity to this impact and adaptative capacity, under natural and human-induced conditions.

The dramatic worldwide regression of seagrass ecosystems is one of the most prevalent paradigms in marine benthic ecology and nature conservation (Short & Wyllie-Echeverria, 1996, 2000; Duarte, 2002; Kenworthy et al., 2006; Orth et al., 2006). An estimate, based upon a two-decade period, has been proposed: 33,000 km^2 lost (Short, 2003). Another estimate indicates a loss of 51,000 km^2 since 1879 (Waycott et al., 2009). On the basis of a conservative estimate of world seagrass meadows of 177,000 km^2 (Spalding et al., 2003), or of a more speculative estimate of 500,000 km^2 (Borum et al., 2004), this would mean a loss ranging between 7 and 29% of their surface area.

The destruction and alteration of seagrass meadows by human activities can be direct, through physical (e.g. burial, uprooting) and chemical damage (e.g. noxious substances), or indirect, through the alteration of the environment (e.g. increase in turbidity, sedimentary deficit), ecosystem organization (e.g. leaf epibiont development) and processes (e.g. over-grazing). Frequently, a single cause (e.g. coastal development) can induce both direct (e.g. burial and uprooting) and indirect (e.g. increased turbidity, epibiont development) destruction (Boudouresque et al., 2009).

The major causes of destruction and alteration of *P. oceanica* meadows are as follows (Pérès, 1984; Boudouresque et al., 1994; Peirano & Bianchi, 1995; Marbà et al., 1996; Moreno et al., 2001; Peirano et al., 2005; Montefalcone et al., 2007a, b; Boudouresque et al., 2009, 2012): (i) Coastal development, including land reclamation, ports, artificial beaches and groynes, which induce the destruction and deterioration of *P. oceanica* meadows through direct burial, increase in turbidity, upstream hyper-sedimentation and downstream erosion (Meinesz et al., 1991; Ruiz & Romero, 2003; Montefalcone et al., 2007b); (ii) Industrial and urban pollution, in particular in the vicinity of large urban centres and sewage outfalls (Pérès, 1984; Pergent-Martini et al., 1995; Duarte, 2002); (iii) Trawling, probably the most severe and worrying cause of *P. oceanica* regression currently in operation (Martín et al., 1997; Pasqualini et al., 2000; González-Correa et al., 2005; Boudouresque et al., 2009); (iv) Fish farming facilities, which constitute a source of pollution and eutrophication due to unconsumed food and fish excretion, in addition to a significant reduction in light intensity (Marbà et al., 2006; Pergent-Martini et al. 2006; Pérez et al., 2008); (v) Mooring (Francour et al., 1999; Milazzo et al., 2004; Montefalcone et al., 2006, 2008); (vi) Brine discharges (Fernández-Torquemada et al. 2005; Sánchez-Lizaso et al., 2008; Sandoval-Gil et al., 2010); (vii) Introduced species. *Caulerpa taxifolia* (Vahl) *C. Agardh* and *C. cylindracea* Sonder (Chlorobionta, Archaeplastida) are capable of invading sparse *P. oceanica* meadows (de Villèle & Verlaque, 1995; Molenaar et al., 2005; Klein & Verlaque, 2008). Dense meadows can be invaded by *Womersleyella setacea*, *Acrothamnion preissii* and/or *Lophocladia lallemandii* (Rhodobionta, Archaeplastida) (Piazzi et al., 2001; Ballesteros et al., 2007) and (viii) Climate change (Mayot et al., 2005; Marbà & Duarte, 2010). In most cases, the anthropogenic regressions of *P. oceanica* meadows cannot be ascribed to a sole cause, but rather to a complex set of direct and indirect causes, the relative weight of which is difficult to unravel (Boudouresque et al., 2009).

The destruction or alteration of a *P. oceanica* meadow obviously concerns all the functional compartments of the ecosystem, in particular those involved in the necromass (Fig. 4), and the ecosystem services they provide (Fig. 8). It also closely concerns the habitats where the *P. oceanica* necromass is exported: beaches and dunes, infralittoral reef habitats, infralittoral sand habitats, circalittoral and bathyal habitats (Fig. 6). Sensitivity is compartment- and impact-dependent (Giakoumi et al., 2015): predatory teleosts are e.g. sensitive to overfishing, while shoot density (leaves and rhizomes) is sensitive to anchoring and trawling. Sensitivity is also habitat-dependent: dead leaves are more sensitive to human activities when cast ashore (on beaches) than when dragged to deep circalittoral and bathyal habitats. Finally, sensitivity is site-dependent: a meadow localized in a marine protected area (MPA), where restrictions are imposed, is less sensitive to, e.g., coastal development and fishing (Astruch et al., 2012; Romero et al., 2012) and the ecosystem services it provides are better preserved, than in areas harbouring e.g. tourism resorts. Regarding adaptative capacity, i.e. the ability of the *P. oceanica* ecosystem and of affiliate habitats, especially the compartments based upon seagrass necromass, to overcome disturbances, it is still more or less speculative and a matter of expert judgement (Giakoumi et al., 2015).

Despite the inhospitable appearance of the *banquettes*, they do not constitute waste or a dangerous product (Chessa et al., 2000). Maintaining them is therefore essential for the protection of the beach (Roig i Munar & Prieto, 2005; Boudouresque, 2010; Cantasano, 2011; Boudouresque et al., 2012; Manca et al., 2013). In many administrative districts, their removal, for the supposed comfort of tourists, by the public authorities, has been matched by a significant regression of the shoreline (Pergent & Kempf, 1993; Pasqualini et al., 1997; Manca et al., 2013). *Banquette* removal may have a strong impact on the beach morphology, e.g. through erosion, the sediment removed during the operation is permanently lost from the beach system and a significant depletion of nutrients and biomass for the coastal ecosystem may occur (Roig i Munar & Prieto, 2005; De Falco et al., 2008; Simeone, 2008; Manca et al., 2013; Simeone & De Falco, 2013). To attempt to compensate for this regression, many coastal districts have started operations of beach replenishment (Boudouresque et al., 2012). The worst aspects of these operations are (i) the increase in water turbidity, when the sediment used contains fine sediment, and (ii) the silting of the meadow when the sediment is swept offshore by storms and currents; if the annual deposit is higher than the ability of orthotropic rhizomes to grow, the vegetative tips are buried and the *P. oceanica* meadow dies (Boudouresque & Jeudy de Grissac, 1983; Manzanera et al., 1998; Alcoverro et al., 2012; Boudouresque et al., 2012; Gera et al., 2014). Both processes (turbidity and silting) result in the short-term decrease in seagrass biomass and the long-lasting (at least two decades) decrease in leaf primary production and starch reserve within rhizomes (Guidetti, 2001, 2004; González-Correa et al., 2008, 2009). In the long term, beach replenishment can result in the withdrawal and the collapse of the meadow (e.g. in Infantes et al., 2009), with the end of the reduction of swell and waves (Fig. 8: box 7) and the increase in beach erosion, a kind of vicious circle (Fig. 9) (Boudouresque, 2010). It is worth noting that, in France, *P. oceanica* is a strictly protected species (*Arrêté du 19 juillet 1988 relatif à la liste des espèces végétales protégées*; Boudouresque, 2013; Boudouresque & Bianchi, 2013): it is forbidden to destroy, transport, sell, buy and use all or part of the plant, living or dead. Hence, the removal of dead leaves from beaches is prohibited, although this prohibition is not always implemented, in the absence of proper controls. Finally, the stay of *P. oceanica* necromass within *banquettes* is for the most part temporary (months or years); sooner or later, it will return to a variety of underwater habitats, participate in the detritus food webs (Mateo et al., 2003; Simeone et al., 2013) and play a role in the nutrient budget of the marine ecosystems, as the leaf litter is a major source of nutrients (Romero et al., 1992; Guala et al., 2006). Fortunately, an increasing number of coastal districts (e.g. Hyères and Le Lavandou in Provence) have stopped removing the *banquette* to a greater or lesser extent. Informing the public, especially children, about why this management measure has been adopted is done verbally, through the local press, by leaflets and by information boards; generally speaking, the public's reaction to this management strategy is favourable and the number of visitors to these 'ecological beaches', when they have been properly informed, has not declined (Zakhama-Sraieb et al., 2011; Boudouresque et al., 2012). Partial removal, i.e. the dumping of removed beached seagrass debris (and the associated sand) at particular sites of the beach, allowing its return to the sea, is also practised, e.g. in Alghero (Sardinia, Italy) (Manca et al., 2013).

The sequestration of carbon within the *P. oceanica* matte constitutes one of the most important services provided by the ecosystem, in the context of mitigation of global climate change; it results in a huge carbon stock accumulated over millennia, estimated to be 2.5–9.6 TgC at Mediterranean scale (Romero et al., 1994; Lo Iacono et al., 2008; MacCord & Mateo, 2010; Pergent et al., 2012; Serrano et al., 2012; Pergent et al., 2014). However, this 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 currents or to waves and swell (Boudouresque et al., 2012). Erosion can also result from human

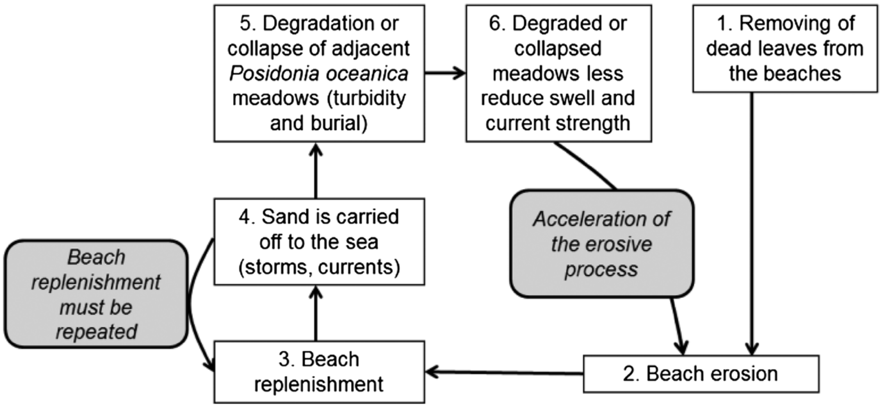

Fig. 9 Consequences of the removal of *P. oceanica* dead leaves from beaches: a kind of vicious circle

activities. Trawling removes the upper layers of rhizomes of the dead *matte*. Anchoring of small leisure boats scars the dead *matte*. The anchors of large boats, such as cruise liners and warships, dig deep trenches and remove huge blocks of *matte* (Ganteaume et al., 2005; Pergent et al., 2014). Dismantling of the matte will increase organic matter remineralisation rates due to exposure to oxygen and return the carbon stored during millennia into the hydrosphere and the atmosphere in the form of carbon dioxide, thus accelerating climate change, in a way similar to that of fossil fuels (Pergent et al., 2014).

Conclusions

The necromass of the *P. oceanica* seagrass meadow is pivotal in the functioning of the ecosystem: *matte*, litter and detritus-feeders. It also plays a role in a number of adjacent habitats, either without moving, within the dead matte habitat, or through exportation of necromass. The stocks of *P. oceanica* necromass, within the meadow (litter), on beaches (*banquettes*) and in adjacent habitats, are closely connected via exchanges between them. The necromass is also involved in ecosystem services, such as protection of beaches from erosion and carbon sequestration. It contributes to the high economic value of the *P. oceanica* meadow, which is among the highest of world ecosystems. The preservation of these meadows, which are vulnerable to an accumulation of human impacts, often working simultaneously, such as coastal development, trawling, anchoring, pollution and climate change, is therefore of paramount importance. This preservation implies not only the protection of the meadow itself, but also that of the in situ and exported necromass stocks such as the *banquettes* on beaches. The reduction by man of any one of these connected stocks threatens all the others and the resulting ecosystem services. In addition, the preservation of the meadows prevents the carbon sequestrated over millennia within the *matte* from being released into the hydrosphere and the atmosphere, in the form of carbon dioxide, thus accelerating climate change.

To date, seagrass ecosystems have mostly been considered in terms of their living compartments, despite awareness of the role and importance of the dead material. The result is that these necromass compartments have been comparatively little studied. In addition, the seagrass necromass and its ‘movements’ between coastal habitats, well beyond the seagrass meadows themselves, is a kind of common denominator, of factor of unity, for the entire coastal system. Quantifying the fluxes of seagrass necromass at the scale of the coastal system, and their contribution to its functioning, constitutes a real challenge for future investigations.

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