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REVIEW ARTICLE

The functioning of an iconic Mediterranean ecosystem, the *Posidonia oceanica* meadow: The keys to a success story

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Abstract

Posidonia oceanica is a seagrass endemic to the Mediterranean Sea, where it is widespread and forms vast meadows down to 25-45 m depth. On the basis of its life history traits and the functioning of the key ecosystem of which it is the ecosystem engineer, the authors attempt to explore the reasons for the overwhelming success of this ecosystem and the ecosystem services it provides in a highly oligotrophic sea. The thickness of the matte, the structure formed by weakly degradable rhizomes and roots and by the sediment that fills the interstices, increases over time, so that the matte sequesters large amounts of carbon. Certain characteristics of the ecosystem make it similar to terrestrial forests, such as the very high plant biomass, the importance of the necromass, the preeminence of the detritivore pathway over the herbivore pathway, and the association of roots with fungi. A sophisticated strategy of collecting, trapping, storing, preserving, and even producing (thanks to association with N_2-fixing bacteria) inorganic nitrogen likely emerged as a response to the extreme oligotrophy of Mediterranean waters. The juxtaposition of two sets of primary producers, the seagrass itself that features weakly palatable and slowly degradable material, and leaf epiphytes that feature highly palatable material, constitute a further key to the success of the ecosystem. Like coral reefs, but through a very different strategy, the *P. oceanica* ecosystem thus supports lush life in nutrient-poor waters. Finally, The *P. oceanica* ecosystem provides humans with a variety of goods and ecosystem services of paramount importance; the most outstanding are (i) carbon sequestration partially mitigating human CO_2 emissions, (ii) the production of organogenic sand derived from the calcareous remains of organisms that lived in the meadow, part of which feeds the beaches, (iii) a significant direct and indirect contribution to fisheries landings, and (iv)

a major role in protecting beaches against erosion, directly through the reduction of wave and swell strength, and indirectly through the deposition of dead leaves on the beach. Overall, by interacting with all other coastal ecosystems, e.g., *via* the exportation of huge amounts of dead leaves, the *P. oceanica* ecosystem constitutes a sort of Mediterranean hub.

Keywords: Carbon sequestration, ecosystem functioning, ecosystem services, Mediterranean Sea, nitrogen, *Posidonia oceanica*

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Introduction

The seagrass *Posidonia oceanica* is endemic to the Mediterranean Sea (Boudouresque and Verlaque 2008). It occurs throughout the Mediterranean, with the exception of the Levantine coast, the northernmost and north-western Adriatic Sea, most of the Gulf of Lions (from the Rhône River mouth to French Catalonia) and the immediate vicinity of the Strait of Gibraltar; very localized populations have been reported from the Sea of Marmara (Meinesz *et al.* 2009; Pergent *et al.* 2012; Öz *et al.* 2014; Azcárate-García *et al.* 2023; Gönülal *et al.* 2023; Mateo-Ramírez *et al.* 2023). All other species of the genus *Posidonia* dwell in Australia, e.g., *P. australis, P. ostenfeldii* and *P. sinuosa* (Kuo *et al.* 1990; Spalding *et al.* 2003).

Posidonia oceanica forms vast meadows between the sea level and 25-45 m depth, depending upon water transparency (Molinier and Picard 1952; Augier and Boudouresque 1979; Boudouresque and Meinesz 1982; Pergent-Martini *et al.* 1999; Tomasello *et al.* 2001; Borg *et al.* 2006; Marbà and Duarte 2010) (Figure 1). For the entire Mediterranean, the surface area of *P. oceanica* meadows has been estimated as between 12,247 km² (Telesca *et al.* 2015) and 19,021 km² (Traganos *et al.* 2022). This represents 23% of the Mediterranean seabed (between the sea level and 50 m depth) (Pasqualini 2005) or 25% (between the sea level and 35 m depth (Agulles *et al.* 2024), and up to 60% in the case of Corsica (between the sea level and 40 m) (Monnier *et al.* 2019; Pergent *et al.* 2019).

Here, on the basis of the life history traits of *Posidonia oceanica* and the functioning of the key ecosystem of which it is the ecosystem engineer, we propose avenues for understanding the overwhelming success of the ecosystem, its resilience, the considerable ecosystem services it provides and the crossroad it constitutes in a highly oligotrophic sea, the Mediterranean.

A very long history

Seagrasses are Magnoliophyta, i.e., flowering plants, with roots and seeds; their ancestors were land plants. It was around 100-70 million years ago that they conquered the marine realm (Kuo and Hartog 2000; Orth *et al.* 2006); they arrived

there with all the 'technology' acquired on land, e.g., flowers, seeds, roots and an efficient conduction system for long-distance transport of sap.

The genus *Posidonia* was present in the Tethys, an east-west ocean that stretched from the Caribbean to eastern Asia. The divergence between Mediterranean and Australian species would have occurred between 40 and 68 Ma ago (Aires *et al.* 2011; Cantasano 2023).

As for *P. oceanica*, it survived the Messinian crises (6.0-5.3 Ma), when the closure of communication with the Atlantic caused the partial drying up of the Mediterranean (Schroeder and Chiggiato 2023; Agiadi *et al.* 2024). The location of the refuges remains unknown: inside the Mediterranean, close to river freshwater inputs preventing hypersalinity, or outside in the nearby Atlantic? (Por 2009; Taviani 2002). Subsequently, *P. oceanica* also survived ~30 glaciation-deglaciation cycles, since 2 Ma, with a cooling of Mediterranean waters of 4-9°C during the last glacial maximum (LGM), more marked in the western than in the eastern Mediterranean; winter sea surface temperature (SST) was locally as low as 7°C (Cacho *et al.* 2002; Kuhlemann *et al.* 2008). At the same time, 18,000-21,000 years ago, the sea level dropped by 120-140 m (Lichter *et al.* 2010; Vacchi *et al.* 2017).

Figure 1. A *Posidonia oceanica* meadow. Cap d'Ail, French Riviera, in 2022. Photo © Thomas Schohn, GIS Posidonie

Overall, *P. oceanica* is a species that generally outcompetes most benthic organisms for substrate occupation in the infralittoral zone (*sensu* Pérès and Picard 1964). Furthermore, contrary to the perceptions of some authors, whose

views are based on a short-term perspective, the species is very resilient to disturbances on a long-term perspective (decades, centuries) and geological scale. Probably excluded, due to low winter temperatures, from the northern Mediterranean during the LGM, *P. oceanica* subsequently reoccupied this area; at the same time, it shifted upwards to follow the rapid Holocene rise in sea level (Boudouresque *et al.* 2021).

Some original features of the *Posidonia oceanica* ecosystem

A characteristic of the *P. oceanica* meadows is that the rhizomes and roots are not very degradable (Piñeiro-Juncal *et al.* 2020) and are preserved, after their death, so that the bottom rises slowly, from 10 to 100 cm per century (Molinier and Picard 1952; Lo Iacomo *et al.* 2008; Mateo *et al.* 2010; Rovere *et al.* 2010; Boudouresque *et al.* 2016) (Figure 2). The structure formed by rhizomes and roots, living and dead, and by the sediment that fills the interstices, is called 'matte' (Molinier and Picard 1952). The thickness of the matte increases over time; it is up to 8 m in eastern Corsica (Monnier *et al.* 2019), over 8 m in the Gulf of Hyères (Provence) (Jeudy de Grissac and Boudouresque 1985) and 16 m in Liguria (Italy) (Rovere *et al.* 2010) (Figure 3).

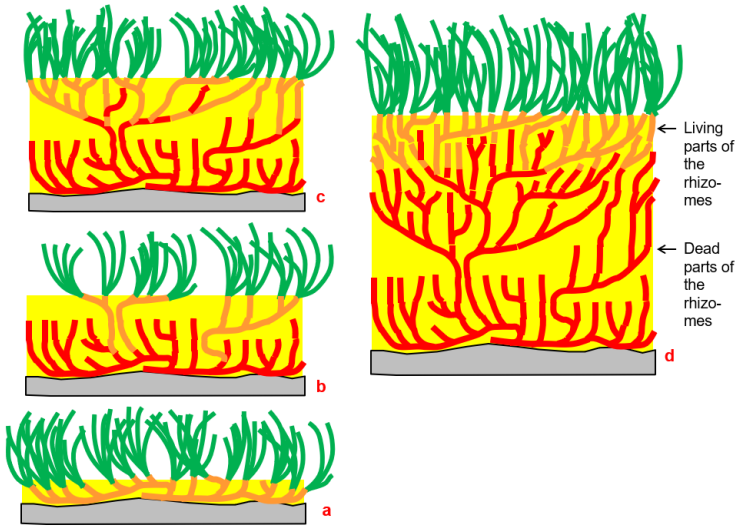

Figure 2. The rising of the *Posidonia oceanica* matte over time. a: Recently established meadow. b, c, d: Autochthonous and allochthonous sediment is trapped by the leaf canopy. To resist being buried, erect orthotropic) rhizomes grow vertically, which results in the thickening of the matte. Green: *P. oceanica* leaves. Ochre: living parts of the rhizomes. Red: dead parts of the rhizomes. Yellow: sediment. Grey: initial substrate (sand or reef).

Four categories of ecosystems can be distinguished on the basis of nutrient availability (proxy: nitrogen – N) and primary production (proxy: chlorophyll – C), both roughly distinguished into low (L) and high (H) levels (Figure 4): LNLC (e.g., Mediterranean pelagic ecosystems and terrestrial forests), HNLC (e.g., Antarctic pelagic ecosystems), HNHC (e.g., upwelling pelagic ecosystems and agricultural systems) and LNHC. Mediterranean *P. oceanica* meadows belong to the latter category (Gobert *et al.* 2002; Boudouresque *et al.* 2006, 2014): a lush and highly productive ecosystem thriving in a highly oligotrophic sea. The mechanisms for this paradox will be analysed below. Another ecosystem shares this feature, the coral reef ecosystem, through an altogether very different strategy (Boudouresque *et al.* 2017a).

Figure 3. An erosion scarp in a *Posidonia oceanica* meadow, in Provence (France), showing the thickness of the *matte*. Note the wrecked leaf shoots, at the foot of the scarp, which shows that erosion of the scarp, due to the hydrodynamics, is still active. Photo © Sandrine Ruitton

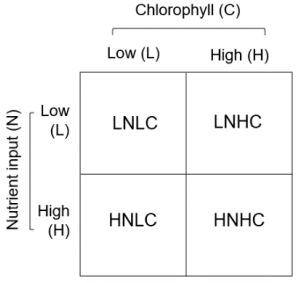

Figure 4. Categories of ecosystems, on the basis of nutrient availability (proxy: nitrogen – N) and primary production (proxy: chlorophyll – C), both roughly distinguished into low (L) and high (H) levels. Redrawn from Boudouresque *et al.* (2014).

The most 'terrestrial' among marine ecosystems

The *P. oceanica* ecosystem can be considered as the most 'terrestrial' among marine ecosystems (Boudouresque *et al.* 2006, 2024). This is due to a set of characteristics considered to be unique in the marine realm, while more common on land, such as the relatively high biomass of primary producers (PPs), the low herbivore pressure, the importance of the detritus-feeder pathway and the most nutrients remaining inside the ecosystem, through their recycling (Boudouresque *et al.* 2014).

(1) The biomass of PPs in the *P. oceanica* ecosystem (rhizomes, roots, leaves, leaf epibiota and rhizome epibiota) can reach values similar to those recorded in land forest ecosystems but far higher than those recorded in the sea, except in some other seagrass ecosystems such as Australian *Posidonia* spp. and Indo-Pacific *Thalassodendron* spp. (Gomis *et al.* 2025). Underground biomass (rhizomes and roots) in the *P. oceanica* ecosystem can reach 1.8 kg Dry Mass (DM)/m² (Guidetti *et al.* 2002), 3.8 kg DM/m² (Francour 1985) and even 4.4 kg DM (Boudouresque and Jeudy de Grissac 1986); it decreases with depth (Olesen *et al.* 2002). Leaf biomass can reach 0.9 kg DM/m² in the Balearic Islands (Barrón and Duarte 2009), 1.3 kg DM/m² in Algeria (Boumaza and Semroud 1995) and 1.6 kg DM/m² in mainland Spain (Romero *et al.* 1998). Overall, including rhizome and leaf epibiota, the biomass of PPs can reach 6.4 kg DM/m² in Corsica (Boudouresque and Jeudy de Grissac 1986).

(2) The herbivore pathway (HP) corresponds to the percentage of direct consumption of the primary production; the detritus-feeder pathway (DFP) corresponds to the percentage of the primary production that is consumed in the form of dead products within the producer ecosystem. Land forest ecosystems are characterized by DFP, while subtidal marine ecosystems are usually characterized by HP. In the *P. oceanica* ecosystem, as in land forest ecosystems, consumption by macro-herbivores, mainly the teleosts *Sarpa salpa* and *Sparisoma cretense* and the sea urchin *Paracentrotus lividus*, usually represents less than 10% of the PP (Mazzella *et al.* 1993; Cebrían *et al.* 1997; Peirano *et al.* 2001; Vizzini 2009; but see Pergent *et al.* 1993; Prado *et al.* 2007; Ferrari *et al.* 2008). As a result, necromass accumulates (Boudouresque *et al.* 2016).

(3) The importance of the DFP in the *P. oceanica* ecosystem is a consequence of the low pressure of herbivores and the resulting availability of necromass (e.g., Gambi *et al.* 1997; Vizzini 2009; Boudouresque *et al.* 2016; Mascart *et al.* 2018). This feature further contributes to bringing it closer to that of land forests.

(4) In land forest ecosystems, most nutrients remain inside the ecosystem, either through their transfer from old leaves before shedding to perennial tissues, then to young leaves, or through recycling of the litter, the soil and the tree roots (Boudouresque *et al.* 2014). In the *P. oceanica* ecosystem, part of the dead leaves

does not remain within the litter and is exported to other ecosystems (e.g., Boudouresque *et al.* 1990; Pergent *et al.* 1994; Fourt and Goujard 2012; Boudouresque *et al*. 2016, 2017a; Oudin and Boudouresque 2023; Di Montanara *et al.* 2024; Boudouresque *et al.* 2025); export also occurs in the form of dissolved organic carbon (DOC) (Champenois *et al.* 2024); however, a variety of mechanisms maximize nutrient conservation within the ecosystem (see below).

Further keys to success

The reasons for the paradox displayed by *P. oceanica*, very high primary production despite the very low nutrient concentrations which characterise most of the Mediterranean, may lie in the functioning of the nutrient machine within the ecosystem (Figure 5).

(1) The extraction by roots of nutrients buried within the sediment; these roots can go down to a depth of at least 70 cm (Francour 1985). (2) The association of roots with fungi (the ascomycete *Posidoniomyces atricolor*) (Vohník *et al.* 2015; 2016, 2017; Borovec and Vohník 2018; Vohník *et al.* 2019) increases their effectiveness in nutrient extraction; such an association is quite common among land trees but unusual in marine environments, with the exception of other seagrass ecosystems, such as the *Zostera marina* meadow (e.g., Ettinger and Eisen, Wainwright *et al.* 2019). (3) The uptake of nutrients both by roots and by leaves; their respective importance varies depending on the sites and the seasons (Kraemer and Mazzella 1996; Invers *et al.* 2002; Gobert *et al.* 2005). (4) The 'luxury uptake' of inorganic nitrogen, taken up in excess with respect to the plant's requirements, at a season when it is relatively abundant in the water column while other primary producers are still not very active due to the lack of light, e.g., in autumn and winter; the nutrients are then stored within the rhizomes for subsequent utilisation (Mateo *et al.* 1997; Invers *et al*. 2000; Lepoint *et al.* 2000; Vizzini *et al.* 2003; Romero 2004); very few primary producers practice luxury uptake in other marine ecosystems (Ricklefs and Miller 2005). (5) The trapping by the *P. oceanica* canopy of POM (Particulate Organic Matter) from the water column and its subsequent remineralization (Duarte *et al.* 1999). (6) Nutrients released by the POM remineralization, together with those from the *P. oceanica* detritus are trapped within the canopy water; the latter acts as a nutrient reservoir for living tissues of *P. oceanica* (Gobert *et al.* 2002). (7) The internal recycling of part of the nutrients from senescent leaves towards young leaves; this provides 20% of *P. oceanica*'s annual nutrient requirement (Lepoint *et al.* 2000); leaf nutrient resorption is a common practice among seagrasses as well as among land trees (Hemminga *et al.* 1999). (8) The presence of N_2-fixing mutualistic bacteria within the rhizosphere; *Candidatus* Celerinatantimonas neptuna provides *P. oceanica* with ammonium and amino acids in exchange for carbohydrates (García-Martínez *et al.* 2005; Mohr *et al.* 2021); N_2 fixation by bacteria is a common feature in the rhizosphere of seagrass ecosystems (Patriquin 1972; Capone 1983; Valiela 1991). (9) The occurrence of N_2-fixing cyanobacteria

within the phyllosphere of seagrasses is also a common feature (Capone and Taylor 1977; Iizumi 1994; Hamisi *et al.* 2009); their occurrence in the *P. oceanica* ecosystem has been suggested (Bethoux and Copin-Montegut 1986; Bethoux *et al.* 1992; Boudouresque *et al.* 2006). Overall, N_2-fixing bacteria of both the rhizosphere and the phyllosphere could account for up to 50% of the nitrogen requirements in seagrasses (Capone 1983; Short *et al.* 1990).

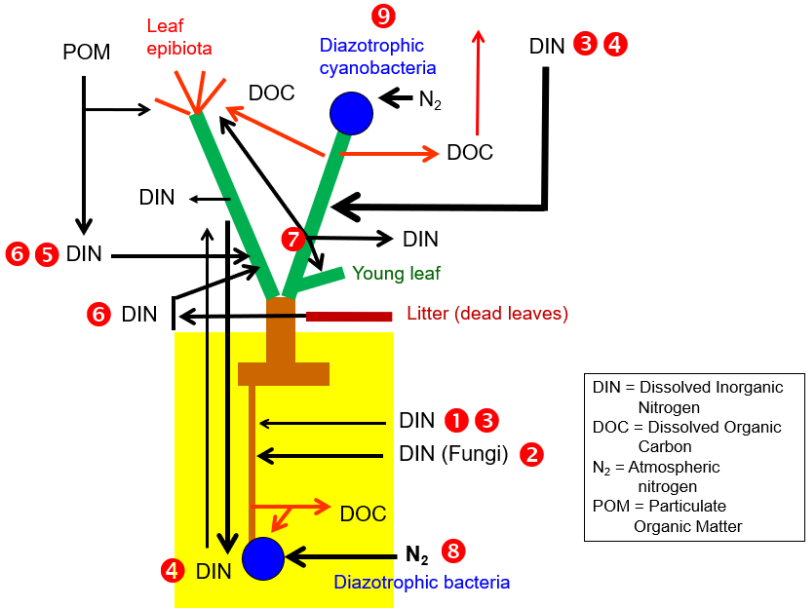

Figure 5. Nutrient and carbon fluxes in the *Posidonia oceanica* ecosystem. Other compartments (leaf epibiota, both autotrophic and heterotrophic) and fluxes (DIN and DOC leaching) are represented. Yellow: the belowground compartment. Green: *P. oceanica* leaves. Light brown: rhizomes and roots. Blue: N2-fixing bacteria. Red numbers: see text. Updated from Boudouresque *et al*. (2006).

This sophisticated strategy of collecting, trapping, storing, preserving, and even producing inorganic nitrogen likely emerged as a response to the extreme oligotrophy of Mediterranean waters. It is possible that the sensitivity of *P. oceanica* to pollution is less direct than indirect: in a polluted environment, nutrient availability is no longer a limiting factor, and the advantage that *P. oceanica* previously enjoyed disappears.

Within the *P. oceanica* ecosystem, there is a juxtaposition of two sets of primary producers. (i) The seagrass itself, which features material that is weakly palatable by herbivores, requires months or years to be degraded and enters the detritus food webs. (ii) Photosynthetic epibiota, belonging to macroalgae (mainly red and brown algae), whose material is generally more easily degraded and quickly enters the herbivore food webs (Boudouresque *et al.* 2006, 2015; Personnic *et al.*

2014) (Figure 6). Most land ecosystems only rely on the first type of primary producers, while most marine benthic photophilous ecosystems are only based upon the second. The first type of primary production ensures a secure, long-term resource that fluctuates little between seasons and years. The second type of production causes seasonal (spring and summer) population blooms of herbivores and their predators, and provides resources for reproduction and juveniles through the food web.

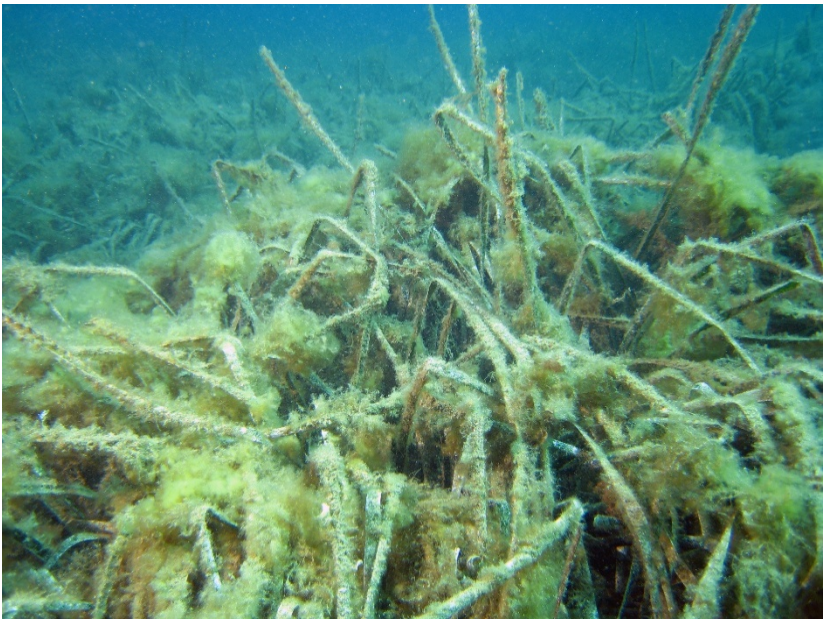

Figure 6. The juxtaposition of two sets of primary producers: the long and narrow seagrass leaves, and the clumps of filamentous macroalgae attached to the leaves. West of Saint-Tropez marina, 16 m depth, August 2007. Photo © Sandrine Ruitton

An interconnected system of gas spaces (aerarium) crosses the whole plant (from leaves to roots), as in all seagrasses (Kuo and McComb 1989; Acunto *et al*. 2000; Klap *et al*. 2000). The aerarium makes possible the recycling of CO_2 (from photorespiration) and the leaking by the roots of O_2 (from photosynthesis) (Pregnall *et al.* 1984; Enriquez *et al.* 2001; Romero 2004; Boudouresque *et al.* 2006).

In a *P. oceanica* meadow, a number of individuals, each originating from a single seed germination event, can coexist; they are genetically distinct and are referred to as 'genets'. Within a 6.4 ha meadow at Ischia Island (Campania, Italy), 126 genets were identified; the largest was 100 m long (Migniaccio *et al.* 2005). A section of rhizome can live between 20 and perhaps 50 years (see Marbà *et al.* 2002; Boudouresque *et al.* 2009); after which it dies so that a genet is fragmented

into several ramets; a ramet is therefore a set of leaf shoots interconnected by live rhizomes, constituting a functional unit. The ramets belonging to a given genet constitute a clone (Boudouresque *et al.* 2009). Within a ramet, photosynthates from a leaf shoot are first exported towards rhizomes, then allocated to other shoots of the ramet (Libes and Boudouresque 1983, 1987; Marbà *et al.* 2002). For a given shoot, this constitutes a kind of insurance: should its photosynthetic budget go into deficit (e.g., due to the overcovering of leaves with epibiota, or to overgrazing), its needs will be supplied by other shoots (Boudouresque *et al.* 2009) (Figure 7).

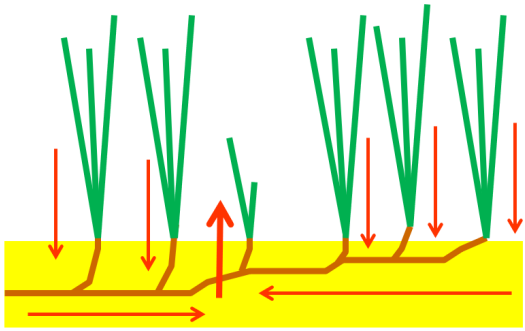

Figure 7. A ramet of *Posidonia oceanica*. Photosynthates are exported towards rhizomes, then allocated to other shoots of the ramet. For the leaf shoot in the centre of the figure, whose photosynthetic budget is in deficit, this constitutes a kind of insurance (red arrows).

A bundle of ecosystem services

The *P. oceanica* ecosystem provides humans with a variety of goods and ecosystem services of paramount importance (e.g., Vassallo *et al.* 2013; Boudouresque *et al.* 2016; El Zrelli *et al.* 2023; Boudouresque *et al.* 2024; Capasso *et al.* 2024; Scemama *et al.* 2024; Addamo *et al.* 2025; Caparrós-Martínez *et al.* 2025; Dentamare *et al.* 2025) (Figure 8).

Among the most outstanding services, carbon sequestration should be placed first (Figure 8: 4). Between 11% and 47% of the primary production is stored within the matte (Pergent *et al.* 1994; Mateo and Romero 1997; Pergent *et al.* 2012; Monnier *et al.* 2022). Large amounts of carbon are therefore sequestered for a long time (at least millennia): 9 to 112 g C/m²/a (Laffoley and Grimsditch 2009). At the scale of the Mediterranean Sea, carbon sequestration is estimated to range between 2.4 and 3.2 Mt C/a (Pergent *et al.* 2019). This carbon sink partly mitigates the anthropogenic release of CO_2: around the Balearic Islands (Spain), the equivalent of 9% of the annual anthropic emissions of CO_2 are trapped in the matte (Maccord and Mateo 2010). Overall, *P. oceanica* is the seagrass which most

sequesters the carbon (Serrano *et al.* 2016), and seagrass beds are among the ecosystems that globally sequester the most carbon, along with peat bogs, mangroves and saltmarshes (Mateo *et al.* 1997; Duarte and Chiscano 1999; Duarte *et al.* 2005; Fourqurean *et al.* 2012; Krause *et al.* 2025).

Another ecosystem service worth highlighting is the role of *P. oceanica* meadows as sand factories (Figure 8: 7). It corresponds to organogenic sand derived from the calcareous remains of organisms that lived in the meadow, e.g., molluscans, sea urchins, bryozoans, foraminiferans, and calcified macroalgae; part of this sand feeds the beaches (Basterretxea *et al.* 2004; De Falco *et al.* 2017; Martín Prieto *et al.* 2018; Simeone *et al.* 2018; Monnier *et al.* 2019; De Luca *et al.* 2020; Bialik *et al.* 2024). In a context where rivers bring less terrigenous sand to the sea, because it is trapped by dams, the relative importance of organogenic sand is increasing (Sharaf El Din 1977; Menéndez *et al.* 2002; Poulos and Collins 2002; Khadr 2003; Syvitski *et al.* 2005; Provansal *et al.* 2009; Boudouresque *et al.* 2022).

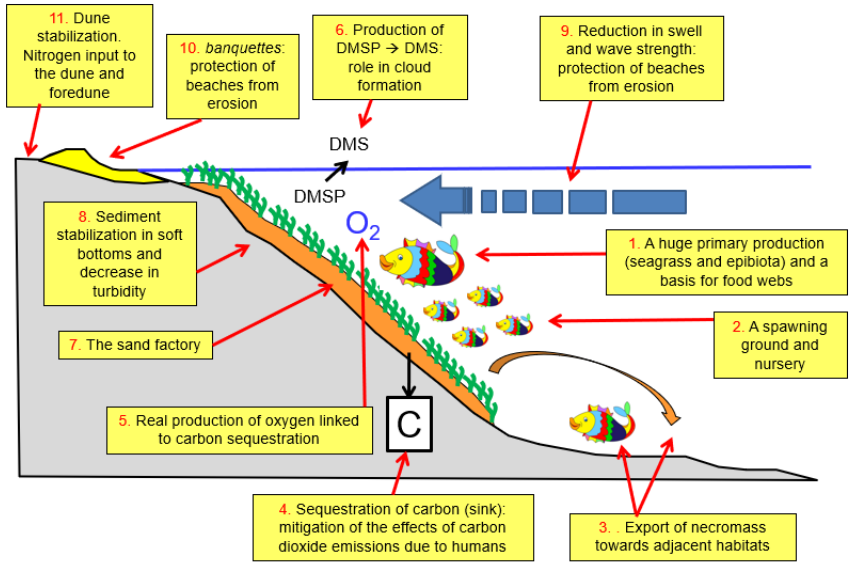

Figure 8. Main ecosystem services provided by the *Posidonia oceanica* ecosystem. Updated from Boudouresque *et al.* (2009).

Species associated with seagrasses (i.e., mainly *P. oceanica*) were estimated to contribute, directly and indirectly, 30-40% to the value of commercial fisheries landings and approximately 29% to recreational fisheries expenditure (Jackson *et al.* 2015) (Figure 8: 1-3).

Finally, *P. oceanica* meadows play a major role in protecting beaches against erosion (Figure 8: 9 and 10). Beach protection is achieved in two ways, directly and indirectly. (i) The direct protection is due to the reduction in swell and wave strength by the meadow (Boudouresque and Jeudy de Grissac 1983; Gacia and Duarte 2001; Cavallaro *et al.* 2010; Sierra *et al.* 2023). The decrease in wave height is between 10 and 40%, on average 24% (Shirinov *et al.* 2025), 30-40% (Jeudy de Grissac and Boudouresque 1985), 60% over a 7 m depth meadow (Infantes *et al.* 2012), or 60-75% over a 2 to 14 m depth meadow (Gacia *et al.* 1999). Unsurprisingly, the degradation of the meadow increases wave height and current speed (El Allaoui *et al.* 2016; Vu 2018). (ii) The indirect protection of beaches is due to the deposition of dead *P. oceanica* leaves, during storms, on the foreshore (Figure 9); these accumulations of dead leaves, 10 to 200 cm thick (up to 300 cm), are called 'banquettes' (De Falco *et al.* 2002; Simeone and De Falco 2013; Boudouresque *et al.* 2017b, 2025; Otero *et al.* 2018; Roig Munar *et al.* 2019; Otero *et al.* 2022; Vandarakis *et al.* 2022; Oudin and Boudouresque 2023; Astudillo-Gutierrez *et al.* 2025a, b; Dentamare *et al.* 2025).

Figure 9. A banquette of *Posidonia oceanica*. Stagnolu beach, south-western Corsica, September 2023. Photo © Charles-François Boudouresque

The hub of Mediterranean coastal ecosystems

The *Posidonia oceanica* ecosystem, by exporting huge quantities of dead leaves to all coastal ecosystems, from beaches to the deep waters of the bathyal zone,

plays a pivotal role in the Mediterranean Sea (Boudouresque *et al.* 2016, 2023) (Figure 10).

Dead leaves constitute a significant food source in the Dune-Beach-Banquette (DBB) ecosystem (Boudouresque *et al.* 2017b, 2025), photophilous reef macroalgal forests (Verlaque and Nédélec 1983; Thibaut *et al.* 2017), sandy infralittoral ecosystems (Dimech *et al.* 2006; Cresson *et al.* 2012; Cresson 2013; Remy *et al.* 2018; Boncagni *et al.* 2019), the coralligenous ecosystem (Boudouresque *et al.* 1990; Astruch *et al.* 2025), coastal detrital bottoms (Astruch *et al.* 2023; Cocozza di Montanara *et al.* 2024) and deep bathyal canyons (Bourcart 1952; Fourt and Goujard 2012) (Figures 11 and 12).

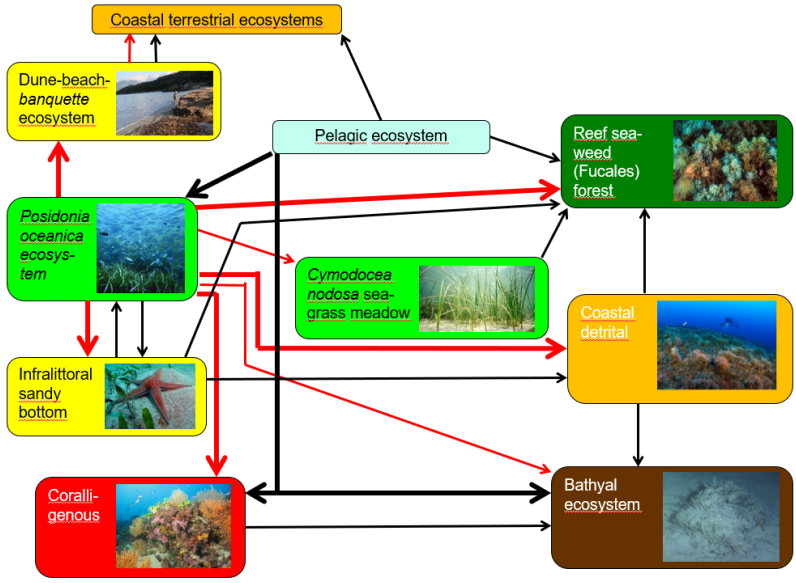

Figure 10. Interactions between the *Posidonia oceanica* ecosystem and some other coastal ecosystems of the Mediterranean. Red arrows: export of dead *P. oceanica* leaves. Black arrows: other flows. From Boudouresque *et al.* (2023).

In addition, the *P. oceanica* ecosystem interacts with these ecosystems *via* a variety of processes, e.g., (i) a spawning area or a nursery for species whose adults dwell in other ecosystems (García-Rubies and Macpherson 1995; Harmelin-Vivien *et al.* 1995; Jimenez *et al.* 1996; Cheminée *et al.* 2021); (ii) a habitat for species whose nursery is located outside; (iii) the importation of fish (e.g., *Chromis chromis* and *Spicara smaris*), plankton and Particulate Organic Matter (POM) from the pelagic ecosystem (Harmelin-Vivien 1982; Templado 1984; Templado *et al.* 2004); (iv) and export of Dissolved Organic Carbon (DOC) to the pelagic ecosystem (Jørgensen *et al.* 1981; Velimirov 1984, 1986; Vizzini 2009) and photophilous reef macroalgal forests (Champenois *et al.* 2024).

Figure 11. Dead leaves and a drift rhizome with two shoots of *Posidonia oceanica*. Toulon Canyon (Provence, France), 363 m depth, April 2010. Some leaves are still green, which means that the pulling out of the rhizome was not very ancient. The scale bar corresponds to the centre of the photo. Photo © Maïa Fourt and Adrien Goujard, courtesy of the authors.

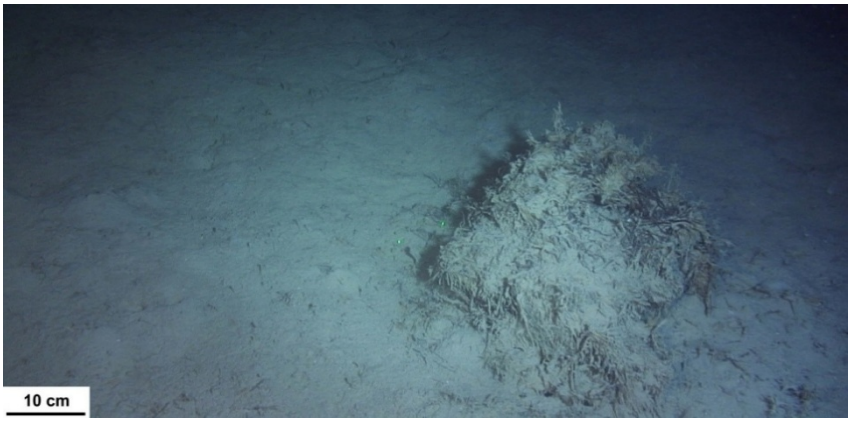

Figure 12. A block of *Posidonia oceanica* matte (20 cm x 20 cm x 10 cm). Juan Canyon (French Riviera), 519 m depth, May 2009. The scale bar corresponds to the centre of the photo. Photo © Maïa Fourt and Adrien Goujard, courtesy of the authors.

Conclusion

The *Posidonia oceanica* ecosystem is a fascinating one. It exhibits unique features, or a unique combination of features, within the biosphere. It has sometimes been described as 'the most terrestrial among marine ecosystems'.

The *P. oceanica* ecosystem is dominant in the infralittoral zone of the Mediterranean Sea, on both hard and soft substrates. Although it has declined due to human activity, mainly coastal development, bottom trawling, anchoring and pollution, around large urban centres (e.g., Meinesz *et al.* 1991; Ramos-Esplá *et al.* 1994; Montefalcone *et al.* 2006, 2007; Boudouresque *et al.* 2009; Montefalcone *et al.* 2009; Holon *et al.* 2015; Telesca *et al.* 2015; El Zrelli *et al.* 2016; Burgos *et al.* 2017; Di Muro *et al.* 2018; Guresen *et al.* 2019; Karayali *et al.* 2022), it is much more resilient than previously thought (Boudouresque *et al.* 2009; Pergent-Martini *et al.* 2013; Boudouresque *et al.* 2021). It has also survived major geological and climatic events, such as the partial drying up of the Mediterranean during the Messinian crises and some thirty glacial and interglacial periods.

We have tried to understand the keys to such a success, which has lasted for millions of years. These keys are numerous. Some refinements were acquired more than 70 million years ago by their terrestrial ancestors. Others were invented more recently, after their colonization of the marine realm. The complex strategy of trapping, preserving, and even producing nutrients in a highly oligotrophic sea, for example, is remarkably effective.

In a shamelessly anthropomorphic way, might we dare suggest that the ultimate success of *P. oceanica* is to have offered humans what they call 'ecosystem services', so that humans will ensure its protection?

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References

Acunto, S., Lyons, A.P., Pouliquen, E. (2000) Some anatomical features of *Posidonia oceanica* leaves and their importance to acoustic scattering. *Biologia Marina Mediterranea* 7(1): 571-574.

Addamo, A.M., La Notte, A., Ferrini, S., Grilli, G. (2025) Marine ecosystem services of seagrass in physical and monetary terms: The Mediterranean Sea case study. *Ecological Economics* 227(108420): 1-13.

Agiadi, K., Hohmann, N., Gliozzi, E., Thivaiou, D., Bosellini, F.R., Taviani, M., Bianucci, G., Collareta, A., Londeix, L., Faranda, C., Bulian, F., Koskeridou, E., Lozar, F., Mancini, A.M., Dominici, S., Moissette, P., Bajo Campos, I., Borghi, E., Iliopoulos, G., Antonarakou, A., *et al.* (2024) The marine biodiversity impact of the Late Miocene Mediterranean salinity crisis. *Science* 385(6712): 986-991.

Agulles, M., Marbà, N., Duarte, C.M., Jordà, G. (2024) Mediterranean seagrasses provide essential coastal protection under climate change. *Scientific Reports* 14(30269): 1-12.

Aires, T., Marbà, N., Cunha, R.L., Kendrick, G.A., Walker, D.I., Serrão, E.A., Duarte, C.M., Arnaud-Haond, S. (2011) Evolutionary history of the seagrass genus *Posidonia. Marine Ecology Progress Series* 421: 117-130.

Astruch, P., Boudouresque, C.F., Cabral, M., Schohn, T., Ballesteros, E., Bellan-Santini, D., Belloni, B., Bianchi, C.N., Cassetti, O., Chevaldonné, P., Fourt, M., Guidetti, P., Hartmann, V., Jacob, É., Le Diréach, L., Michez, N., Montefalcone, M., Morri, C., Nérini, D., Pérez, T., *et al.* (2025) An ecosystem-based index for Mediterranean coralligenous reefs: A protocol to assess the quality of a complex key habitat. *Marine Pollution Bulletin* 220(118375): 1-28.

Astruch, P., Orts, A., Schohn, T., Belloni, B., Ballesteros, E., Bănaru, D., Bianchi, C.N., Boudouresque, C.F., Changeux, T., Chevaldonné, P., Harmelin, J.G., Michez, N., Monnier, B., Morri, C., Ruitton, S., Thibaut, T., Vacelet, J., Verlaque, M., Daniel, B. (2023) Ecosystem-based assessment of a widespread Mediterranean marine habitat: The Coastal Detrital Bottoms, with a special focus on epibenthic assemblages. *Frontiers in Marine Science* 10(1130540): 1-25.

Astudillo-Gutierrez, C., Pavo-Fernandez, E., Gracia, V., Sierra, J.P., Llull, T., Mosso, C., Sanchez-Artus, X., Sanchez-Arcilla, A. (2025b) *Posidonia oceanica* banquette accumulations in southern Catalonia: Management approaches and key parameters for coastal protection. *Frontiers in Marine Science* 121(681826): 1-19.

Astudillo-Gutierrez, C., Sierra, J.P., Mösso, C., Gracia, V. (2025a) Impact of banquette structures on a sandy beach profile: Laboratory experiments. *Coastal Engineering* 202(104815): 1-14.

Augier, H., Boudouresque, C.F. (1979) Initial observations of the *Posidonia oceanica* seagrass meadows and coastal detrital bottoms of Île du Levant (Mediterranean Sea, France), using the French Navy's Griffon submarine. *Travaux Scientifiques du Parc National de Port-Cros* 5: 141-153 (in French).

Azcárate-García, T., Beca-Carretero, P., Brun, F.G. (2023) Plant and meadow structure characterisation of *Posidonia oceanica* in its westernmost distribution range. *Diversity* 15(101): 1-10.

Barrón, C., Duarte, C.M. (2009) Dissolved organic matter release in a *Posidonia oceanica* meadow. *Marine Ecology Progress Series* 374: 75-84.

Basterretxea, G., Orfila, A., Jordi, A., Lynett, P., Liu, P.L.F., Duarte, C.M., Tintoré, J. (2004) Seasonal dynamics of microtidal pocket beach with *Posidonia oceanica* seabeds Mallorca, Spain). *Journal of Coastal Research* 20(4): 1155-1164.

Bethoux, J.P., Copin-Montegut, G. (1986) Biological fixation of atmospheric nitrogen in the Mediterranean Sea. *Limnology & Oceanography* 31(6): 1353-1358.

Bethoux, J.P., Morin, P., Madec, C., Gentili, B. (1992) Phosphorus and nitrogen behaviour in the Mediterranean Sea. *Deep-Sea Research* 39(9): 1641-1654.

Bialik, O.M., Coletti, G., Berndt, C., Schmidt, M., Micallef, A. (2024) Controls on mesophotic carbonate facies and sediment distribution across the Maltese shelf, central Mediterranean Sea. *Facies* 70(16): 1-19.

Boncagni, P., Rakaj, A., Fianchini, A., Vizzini, S. (2019) Preferential assimilation of seagrass detritus by two coexisting Mediterranean Sea cucumbers: *Holothuria polii* and *Holothuria tubulosa*. *Estuarine, Coastal and Shelf Science* 231(106464): 1-9.

Borg, J.A., Micallef, M.A., Schembri, P.J. (2006) Spatio-temporal variation in the structure of a deep water *Posidonia oceanica* meadow assessed using non-destructive techniques. *Marine Ecology* 27: 320-327.

Borovec, A., Vohník, M. (2018) Ontogenic transition from specialized root hairs to specific root-fungus symbiosis in the dominant Mediterranean seagrass *Posidonia oceanica. Scientific Reports* 8(10773): 1-11.

Boudouresque, C.F., Astruch, P., Belloni, B., Blanfuné, A., Francesiaz, C., Maury, M., Médail, F., Paradis, G., Perret-Boudouresque, M., Piazza, C., Ponel, P., Sindou, P., Thibaut T. (2025) The Mediterranean dune-beach-banquette ecosystem, its pivotal role in land-sea coupling and the functioning of coastal systems, and some related management issues. *Sustainability* 17(4556): 1-31.

Boudouresque, C.F., Bănaru, D., Changeux, T. (2022) Rivers, floods, beaches and coastal habitats: A plea for an integrated approach in the Mediterranean. *Scientific Reports of Port-Cros National Park* 36: 43-57.

Boudouresque, C.F., Bernard, G., Pergent, G., Shili, A., Verlaque, M. (2009) Regression of Mediterranean seagrasses caused by natural processes and anthropogenic disturbances and stress: A critical review. *Botanica Marina* 52(5): 395-418.

Boudouresque, C.F., Bianconi, C.H., Meinesz, A. (1990) Live *Posidonia oceanica* in a coralligenous algal bank at Sulana Bay, Corsica. *Rapports et Procès-Verbaux des Réunions de la Commission Internationale pour l'Exploration Scientifique de la Méditerranée* 32(1): 11.

Boudouresque, C.F., Blanfuné, A., Changeux, T., Pergent, G., Perret-Boudouresque, M., Ruitton, S., Thibaut, T. (2023) Marine biodiversity in the Mediterranean in the era of global warming. *La Mer* 61: 189-231.

Boudouresque, C.F., Blanfuné, A., Harmelin-Vivien, M., Personnic, S., Ruitton, S., Thibaut, T., Verlaque, M. (2017a) Where Seaweed Forests Meet Animal Forests: The Examples of Macroalgae in Coral Reefs and the Mediterranean Coralligenous Ecosystem. In: Marine Animal Forests, (eds., Rossi, S., Bramanti, L., Gori, A., Orejas, C.), Springer International Publishing Switzerland, pp. 369-396.

Boudouresque, C.F., Blanfuné, A., Pergent, G., Thibaut, T. (2021) Restoration of seagrass meadows in the Mediterranean Sea: A critical review of effectiveness and ethical issues. *Water* 13(1034): 1-35.

Boudouresque, C.F., Jeudy de Grissac, A. (1983) *Posidonia oceanica* seagrass meadows in the Mediterranean: Interactions between the plant and the sediment. *Journal de Recherches Océanographiques* 8(2-3): 99-122 (in French).

Boudouresque, C.F., Jeudy de Grissac, A. (1986) Biomass in the *Posidonia oceanica* meadow. *Travaux Scientifiques du Parc Naturel Régional et des Réserves Naturelles de Corse* 2: 14-15 (in French).

Boudouresque, C.F., Mayot, N., Pergent, G. (2006) The outstanding traits of the functioning of the *Posidonia oceanica* seagrass ecosystem. *Biologia Marina Mediterranea* 13(4): 109-113.

Boudouresque, C.F., Meinesz, A. (1982) Discovery of the *Posidonia* seagrass meadow. *Cahiers du Parc Natlional de Port-Cros* 4: 1-79 (in French).

Boudouresque, C.F., Pergent, G., Pergent-Martini, C., Ruitton, S., Thibaut, T., Verlaque, M. (2016) The necromass of the *Posidonia oceanica* seagrass meadow: Fate, role, ecosystem services and vulnerability. *Hydrobiologia* 781: 25-42.

Boudouresque, C.F., Perret-Boudouresque, M., Ruitton, S., (2024) A Forest under the Sea: The *Posidonia oceanica* Seagrass Meadow. In: Pour que vive la Méditerranée – Vers une économie bleue durable, (eds., Demeester M.L., Mercier, V., Vicente, N.), Presses de l'Université d'Aix-Marseille (PUAM) publ., Aix-en Provence, pp. 55-71 (in French).

Boudouresque, C.F., Personnic, S., Astruch, P., Ballesteros, E., Bellan-Santini, D., Bonhomme, P., Botha, D., Feunteun, E., Harmelin-Vivien, M., Pergent, G., Pastor, J., Poggiale, J.C., Renaud, F., Thibaut, T., Ruitton, S. (2015) Ecosystem-based versus Species-based Approach for Assessment of the Human Impact on the Mediterranean Seagrass *Posidonia oceanica*. In: Marine Productivity: Perturbations and Resilience of Socio-ecosystems, (eds., Ceccaldi, H., Hénocque, Y., Koike, Y., Komatsu, T., Stora, G., Tusseau-Vuillemin, M.H.), Springer International Publishing Switzerland, pp. 235-241.

Boudouresque, C.F., Ponel, P., Astruch, A., Barcelo, A., Blanfuné, A., Geoffroy, D., Thibaut, T. (2017b) The high heritage value of the Mediterranean sandy beaches, with a particular focus on the *Posidonia oceanica* '*banquettes*': A review. *Scientific Reports of Port-Cros National Park* 31: 23-70.

Boudouresque, C.F., Ruitton, S., Bianchi, C.N., Chevaldonné, P., Fernandez, C., Harmelin-Vivien, M., Ourgaud, M., Pasqualini, V., Perez, T., Pergent, G., Thibaut, T., Verlaque, M. (2014) Terrestrial versus marine diversity of ecosystems. And the winner is: The marine realm. In: Proceedings of the 5th Mediterranean Symposium on Marine Vegetation (Portorož, Slovenia, 27-28 October 2014), (eds., Langar, H., Bouafif, C., Ouerghi, A.), RAC/SPA publ., Tunis, pp. 11-25.

Boudouresque, C.F., Verlaque, M. (2008) Does the seagrass *Posidonia* really occur in Madagascar? *Phycologia* 47(4): 435-436.

Boumaza, S., Semroud, R. (1995) Seasonal variations in biomass (leaves and epiphytes) of *Posidonia oceanica* (L.) Delile in the seagrass meadow of Kouali cove (Tipaza), Algeria: Preliminary data. *Rapports et Procès-Verbaux des*

Réunions de la Commission Internationale pour l'Exploration Scientifique de la Méditerranée 34: 21 (in French).

Bourcart, J. (1952) Oceanographic mission on the continental shelf of the coast of Provence, in April 1952, aboard the aviso 'Ingénieur Elie Monnier'. *Bulletin d'Information* (Service Hydrographique de la Marine), 4(7): 279-282 + 1 map.

Burgos, E., Montefalcone, M., Ferrari, M., Paoli, C., Vassallo, P., Morri, C., Bianchi, C.N. (2017) Ecosystem functions and economic wealth: Trajectories of change in seagrass meadows. *Journal of Cleaner Production* 168: 1108-1119.

Cacho, I., Grimalt, J.O., Canals, M. (2002) Response of the Western Mediterranean Sea to rapid climatic variability during the last 50,000 years: A molecular biomarker approach. *Journal of Marine Systems* 33-34: 253-272.

Cantasano, N. (2023) Back to the Sea: The long and winding road of the seagrass species *Posidonia oceanica*. *Advances in Environmental and Engineering Research* 4(1): 1-9.

Caparrós-Martínez, J.L., Martínez-Vásquez, R.M., Valenciano, J. de P. (2025) Future challenges in the conservation and valuation of environmental services provided by the seagrass meadows of "*Posidonia oceanica*". *Marine Policy* 175(106630): 1-11.

Capasso, L., Buonocore, E., Franzese, P.P., Russo, G.F. (2024) The scientific literature on *Posidonia oceanica* meadows and related ecosystem services. *Ecological Questions* 35(1): 1-14.

Capone, D.G. (1983) N2 fixation in seagrass communities. *Marine Technology Society Journal* 17(2): 32-37.

Capone, D.G., Taylor, B.F., (1977) Nitrogen fixation (acetylene reduction) in the phyllosphere of *Thalassia testudinum. Marine Biology* 40: 19-28.

Cavallaro, L., Lo Re, C., Paratore, G., Viviano, A., Foti, E. (2010) Response of *Posidonia oceanica* plants to wave motion in shallow waters – Preliminary experiment results. In: Proceedings of the 32nd Conference on Coastal Engeneering, Shanghai, China.

Cebrián, J., Duarte, C.M., Marbà, N., Enríquez, S. (1997) Magnitude and fate of the production of four co-occurring Western Mediterranean seagrass species. *Marine Ecology Progress Series* 155: 29-44.

Champenois, W., Lepoint, G., Borges, A.V. (2024) Community gross primary production and respiration in epilithic macroalgae and *Posidonia oceanica*

macrophytodetritus accumulation in the Bay of Revellata (Corsica). *Estuarine, Coastal and Shelf Science* 309(108971): 1-11.

Cheminée, A., Le Diréach, L., Rouanet, É, Astruch, P., Goujard, A., Blanfuné, A., Bonhomme, D., Chassaing, L., Jouvenel, J.Y., Ruitton, S., Thibaut, T., Harmelin-Vivien, M. (2021) All shallow coastal habitats matter as nurseries for Mediterranean juvenile fish. *Scientific Reports* 11(14631): 1-17.

Cocozza di Montanara, A., Semprucci, F., Rendina, F., Russo, G.F., Sandulli, R. (2024) Re-discovering macerating *Posidonia oceanica* bottoms: Characterization of meiofaunal community inhabiting a peculiar Mediterranean habitat. *Estuarine, Coastal and Shelf Science* 309(108956): 1-11.

Cresson, P. (2013) Trophic Functioning of the Artificial Reefs of Prado Bay (Marseille, France): Origin and Fate of Organic Matter. Doctoral thesis, Aix-Marseille University, Marseille (in French).

Cresson, P., Ruitton, S., Fontaine, M.F., Harmelin-Vivien, M. (2012) Spatio-temporal variation of suspended and sedimentary organic matter quality in the Bay of Marseilles (NW Mediterranean) assessed by biochemical and isotopic analyses. *Marine Pollution Bulletin* 64: 1112-1121.

De Falco, G., Baroli, M., Simeone, S., Piergallini, G. (2002) The Removal of Posidonia from Beaches: Consequences for Coastal Stability. Fondazione IMC – Centro Marino Internazionale - ONLUS publ., Torregrande Oristano, Italy (in Italian).

De Falco, G., Molinaroli, E., Conforti, A., Simeone, S., Tonielli, R. (2017) Biogenic sediments from coastal ecosystems to beach-dune systems: implications for the adaptation of mixed and carbonate beaches to future sea level rise. *Biogeoscience Discussions* 20: 1-27.

De Luca, M., Chaiallah, A., Andreucci, S., Cossu, G., Santonastaso, A., Sechi, D., Stelletti, M., Pascucci, V. (2020) Seafloor map of the Alghero Bay (Sardinia, Italy). *Journal of Maps* 16(2): 669-679.

Dentamare, I., Capasso, L., Chianese, E., Calicchio, R., Franzese, P.P., Grande, U., Russo, G.F., Buonocore, E. (2025) Ecological implications of *Posidonia oceanica* banquette removal: Potential loss of natural capital and ecosystem services. *Water* 17(1362): 1-14.

Di Montanara, A.C., Semprucci, F., Rendina, F., Russo, G. F., Sandulli, R. (2024) Re-discovering macerating *Posidonia oceanica* bottoms: Characterization of meiofaunal community inhabiting a peculiar Mediterranean habitat. *Estuarine, Coastal and Shelf Science* 309(108956): 1-11.

Di Muro, S., Porta, M., Pusceddu, N., Frongia, P., Passarella, M., Ruju, A., Buosi, C., Ibba, A. (2018) Geomorphological processes of a Mediterranean urbanized beach (Sardinia, Gulf of Cagliari). *Journal of Maps* 14(2): 114-122.

Dimech, M., Borg, J.A., Schembri, P.J. (2006) Motile macroinvertebrate assemblages associated with submerged *Posidonia oceanica* litter accumulations. *Biologia Marina Mediterranea* 13(4): 130-133.

Duarte, C.M., Benavent, E., Sanchez, M. del C. (1999) The microcosm of particle within seagrass *Posidonia oceanica* canopies. *Marine Ecology Progress Series* 181: 289-295.

Duarte, C.M., Chiscano, C.L. (1999) Seagrass biomass and production: A reassessment. *Aquatic Botany* 65: 159-174.

Duarte, C.M., Middelburg, J.J., Caraco, N. (2005) Major role of marine vegetation on the oceanic carbon cycle. *Biogeoscience* 2: 1-8.

El Allaoui, N., Serra, T., Colomer, J., Soler, M., Casamitjana, X., Oldham, C. (2016) Interactions between fragmented seagrass canopies and the local hydrodynamics. *Plos OnE* 11(5): e0156264.

El Zrelli, R., Courjault-Radé, P., Gallai, N., Rabaoui, L., Mansour, L., Bejaoui, N. (2016) Evaluation of the ecosystem service provided by *Posidonia* seagrass meadows in the Gulf of Gabès. *Rapports de la Commission Internationale de la Mer Méditerranée* 41: 512 (in French).

El Zrelli, R., Hcine, A., Yacoubi, L., Roa-Ureta, T.H., Gallai, N., Castet, S., Grégoire, M., Courjault-Radé, P., Rabaoui, L.J. (2023) Economic losses related to the reduction of *Posidonia* ecosystem services in the Gulf of Gabes (Southern Mediterranean Sea). *Marine Pollution Bulletin* 186(114418): 1-9.

Enriquez, S., Marba, N., Duarte, C.M., Tussenbroek, B.I. van, Reyes-Zavala, G. (2001) Effect of seagrass *Thalassia testudinum* on sediment redox. *Marine Ecology Progress Series* 219: 149-158.

Ettinger, C.L., Eisen, J.A. (2019) Characterization of the mycobiome of the seagrass, *Zostera marina*, reveals putative associations with marine chytrids. *Frontiers in Microbiology* 10(2476).

Ferrari, B., Raventos, N., Planes, S. (2008) Assessing effects of fishing prohibition on *Posidonia oceanica* seagrass meadows in the Marine Natural Reserve of Cerbère-Banyuls. *Aquatic Botany* 88: 295-302.

Fourqurean, J.W., Duarte, C.M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M.A., Apostolaki E.T., Kendrick G.A., Krause-Jensen D., Mcglathery K.J., Serrano, O. (2012) Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience* 5(7): 505-509.

Fourt, M., Goujard, A. (2012) Scientific report of the MESDEACAN campaign (Heads of continental Mediterranean canyons) November 2008-April 2010. Partenariat Agence des Aires marines protégées – GIS Posidonie, GIS Posidonie publ., Marseille.

Francour, P. (1985) Root and rhizome biomass of *Posidonia oceanica* beds. *Rapports et Procès-Verbaux des Réunions de la Commission Internationale pour l'Exploration Scientifique de la Méditerranée* 29(5): 183-185.

Gacia, E., Duarte, C.M. (2001) Sediment retention by a Mediterranean *Posidonia oceanica* meadow: the balance between deposition and resuspension. *Estuarine, Coastal and Shelf Science* 52: 505-514.

Gacia, E., Granata, T.C., Duarte, C.M. (1999) An approach to measurement of particle flux and sediment retention within seagrass (*Posidonia oceanica*) meadows. *Aquatic Botany* 65: 255-268.

Gambi, M.C., Lorenti, M., Bussotti, S., Guidetti, P. (1997) Borers in *Posidonia oceanica* scales: Taxonomical composition and occurrence. *Biologia Marina Mediterranea* 4(1): 384-487.

García-Martínez, M., Kuo, J., Kilminster, K., Walker, D., Rosseló-Mora R., Duarte, C.M. (2005) Microbial colonization in the seagrass *Posidonia* spp. roots. *Marine Biology Research* 1(6): 388-395.

García-Rubies, A., Macpherson, E. 1995. Substrate use and temporal pattern of recruitment in juveniles fishes of the Mediterranean littoral. *Marine Biology* 124: 35-42.

Gobert, S., Laumont, N., Bouquegneau, J.M. (2002) *Posidonia oceanica* meadow: A low nutrient high chlorophyll (LNHC) system? *BMC Ecology* 2(9): 1-12.

Gobert, S., Lejeune, P., Lepoint, G., Bouquegneau, J.M. (2005) C, N, P concentrations and requirements of flowering *Posidonia oceanica* shoots. *Hydrobiologia* 533: 253-259.

Gomis, E., Strydom, S., Foster, N.R., Montemayor, D., Mateo, M.A., Serrano, E., Inostroza, K., McCallum, R., Lafratta, A., Webster, C.L., O'dea, C.M., Said, N.E., Dunham, N., Bernasconi, R., Werner, A., Vitelli, F., Puigcorbé, V., D'cruz, A.,

Salinas, C., McMahon, K.M., *et al.* (2025) Global estimates of seagrass blue carbon stocks in biomass and net primary production. *Nature Communications* 16(9530): 1-12.

Gönülal, O., Gürses, R.K., Hisli, O., Gülenç, Z. (2023) Further extension and fine-scale coverage area of the *Posidonia oceanica* in Paşalimanı Island and the Kapıdağ Peninsula, the Sea of Marmara. *Journal of Black Sea/Mediterranean Environment* 29(3): 283-290.

Guidetti, P., Lorenti, M., Buia, M.C., Mazzella, L. (2002) Temporal dynamics and biomass partitioning in three Adriatic seagrass species: *Posidonia oceanica, Cymodocea nodosa, Zostera marina*. *PSZN: Marine Ecology* 23(1): 51-67.

Guresen, A., Guresen, S.O., Sari, E., Pergent, G., Aktan, Y. (2019) Regression trend of *Posidonia oceanica* in a pilot region (Turkey) within the monitoring programme of the Med*Posidonia*. In: Proceedings of the 6th Mediterranean symposium on marine vegetation, Antalya, Turkey, 14-15 January 2019, (eds., Langar, H., Ouerghi, A.), RAC/SPA publ., Tunis, Tunisia, pp. 59-63.

Hamisi, M.I., Lyimo, T.J., Muruke, M.H.S., Bergam, B. (2009) Nitrogen fixation by epiphytic and epibenthic diazotrophs associated with seagrass meadows along the Tanzanian coast, Western Indian Ocean. *Aquatic Microbial Ecology* 57: 33-42.

Harmelin-Vivien, M. (1982) Ichtyofaune des herbiers de posidonies du Parc national de Port-Cros: I. Composition et variations spatio-temporelles. *Trav. Sci. Parc Natl. Port-Cros* 8: 69-92.

Harmelin-Vivien, M.L., Harmelin, J.G., Leboulleux, V. (1995) Microhabitat requirements for settlement of juvenile sparid fishes on Mediterranean rocky shores. *Hydrobiologia* 300-301: 309-320.

Hemminga, M.A., Marbà, N., Stapel, J. (1999) Leaf nutrient resorption, leaf lifespan and the retention of nutrients in seagrass systems. *Aquatic Botany* 65: 141-158.

Holon, F., Boissery, P., Guilbert, A., Freschet, E., Deter, J. (2015) The impact of 85 years of coastal development on shallow seagrass beds (*Posidonia oceanica* L. (Delile) in South Eastern France: A slow but steady loss without recovery. *Estuarine, Coastal and Shelf Science* 165: 204-212.

Iizumi, H. (1994) Nitrogen Fixation, a Nitrogen Input to a Tropical Seagrass Bed. In: Developmental Processes and Material Flow in Tropical Seagrass Beds, (ed., Koike), Univ. Tokyo publ., Tokyo, Japan, pp. 31-39.

Infantes, E., Orfila, A., Simarro, G., Terrados, J., Luhar, M., Nepf, H. (2012) Effect of a seagrass (*Posidonia oceanica*) meadow on wave propagation. *Marine Ecology Progress Series* 456: 63-72.

Invers, O., Pérez, M., Romero, J. (2000) Experimental nitrogen enrichment in *Posidonia oceanica*: Effects on nitrogen metabolism and carbon storage. *Biologia. Marina Mediterranea* 7(2): 67-70.

Invers, O., Pérez, M., Romero, J. (2002) Seasonal nitrogen speciation in temperate seagrass *Posidonia oceanica* (L.) Delile. *Journal of Experimental Marine Biology and Ecology* 273: 219-240.

Jackson, E.L., Rees, S.E., Wilding, C., Attrill, M.J. (2015) Use of a seagrass residency index to apportion commercial fishery landing values and recreation fisheries expenditure to seagrass habitat service. *Conservation Biology* 29(3): 899-909.

Jeudy de Grissac, A., Boudouresque, C.F. (1985) Role of seagrass meadows in coastal sediment movements: *Posidonia oceanica* meadows. In: Colloque franco-japonais d'Océanographie, Marseille 1: 143-151 (in French).

Jimenez, S., Cano, R., Bayle, J., Ramos, A., Sanchez Lizaso, J.L. (1996) *Posidonia oceanica* (L.) Delile meadows as a protection zone for juveniles of commercially important species. *Real Sociedad Española de Historia Natural* tomo extraordinario 375-378 (in Spanish).

Jørgensen, N.O.G., Blackburn, T.H., Henriksen, K., Bay, D. (1981) The importance of *Posidonia oceanica* and *Cymodocea nodosa* as contributors of free amino acids in water and sediment of seagrass beds. *Marine Ecology* 2(2): 97-112.

Karayali, O., Akçali, B., Bizsel, K.C., Kaboğlu, G. (2022) Need of reference conditions for comparable monitoring of *Posidonia oceanica* at the eco-regional scale including the sliding baseline syndrome: A discussion over Foca Sepa. In: 7th Mediterranean symposium on marine vegetation, Genoa, 19-20 September 2022, RAC/SPA publ., Tunis, Tunisia, pp. 60-65.

Khadr, A.M. (2003) Evolution of the Nile Deposits Input during the Quaternary and its Effect on Egyptian Coastline. In: Human Records of Recent Geological Evolution in the Mediterranean Basin – Historical and Archeological Evidence. CIESM Workshop Monographs 24, CIESM publ., Monaco, pp. 25-28.

Klap, V.A., Hemminga, M.A., Boon, J.J. (2000) Retention of lignin in seagrasses: Angiosperms that returned to the sea. *Marine Ecology Progress Series* 194: 1-11.

Kraemer, G.P., Mazzella, L. (1996) Nitrogen assimilation and growth dynamics of the Mediterranean seagrasses *Posidonia oceanica, Cymodocea nodosa,* and *Zostera noltii*. In: Seagrass Biology: Proceedings of an International Workshop, (eds., Kuo, J., Phillips, R.C., Walker, D.I., Kirkman, H.), Australia, pp. 181-190.

Krause, J.R., Cameron, C., Arias-Ortiz, A., Cifuentes-Jara, M., Crooks, S., Dahl, M., Friess, D.A., Kennedy, H., Lim, K.E., Lovelock, C.E., Marbà, N., McGlathery, K.J., Oreska, M.P.J., Pidgeon, E., Serrano, O., Vanderklift, M.A., Wong, L.W., Yaakub, S.M., Fourqurean, J.W. (2025) Global seagrass carbon stock variability and emissions from seagrass loss. *Nature Communications* 16(3798): 1-9.

Kuhlemann, J., Rohling, E.J., Krumrei, I., Kubik, P., Ivy-Ochs, S., Kucera, M. (2008) Regional synthesis of Mediterranean athmospheric circulation during the Last Glacial Maximum. *Science* 321: 1338-1340.

Kuo, J., den Hartog, C. (2000) Seagrasses: A profile of an ecological group. *Biologia Marina Mediterranea* 7(2): 3-17.

Kuo, J., James, S.H., Kirkman, H., den Hartog, C. (1990) Chromosome numbers and their systematic implications in Australian marine angiosperms: The Posidoniaceae. *Plant Systematics and Evolution* 171: 199-204.

Kuo, J., McComb, A.J. (1989) Seagrass Taxonomy, Structure and Development. In: Biology of Seagrasses. A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region, (eds., Larkum, A.W.D., McComb, A.J., Shepherd, S.A.), Elsevier publ., Amsterdam, pp. 6-73.

Laffoley, D., Grimsditch, G. (eds.) (2009) The Management of Natural Coastal Carbon Sinks. IUCN Publ., Gland, Switzerland.

Lepoint, G., Gobert, S., Bouquegneau, J.M. (2000) A ^{15}N tracer study of N recycling by the seagrass *Posidonia oceanica. Biologia Marina Mediterranea* 7(2): 87-90.

Libes, M., Boudouresque, C.F. (1983) In situ evidence of long-distance photosynthetic transport in *Posidonia oceanica* (marine phanerogam) and its epiphytes: Preliminary note. *Travaux Scientifiques du Parc National de Port-Cros* 9: 75-87 (in French).

Libes, M., Boudouresque, C.F. (1987) Uptake and long-distance transport of carbon in the marine phanerogam *Posidonia oceanica*. *Marine Ecology Progress Series* 38: 177-186.

Lichter, M., Zviely, D., Klein, M., Sivan, D. (2010) Sea-level Changes in the Mediterranean: Past, Present and Future – A Review. In: Seaweeds and Their Role in Globally Changing Environments, (eds., Israel, A., Einav, R., Seckbach, J.), Springer publ., Dordrecht, pp. 5-17.

Lo Iacono, C., Mateo, M.A., Gràcia, E., Guasch, L., Carbonell, R., Serrano, L., Serrano, O., Dañobeita, J. (2008) Very high-resolution seismo-acoustic imaging of seagrass meadows (Mediterranean Sea): Implications for carbon sink estimates. *Geophysical Research Letters* 35(L18601): 1-5.

Maccord, F., Mateo, M.A. (2010) Estimating the size of the carbon sink represented by *Posidonia oceanica* meadows along the coasts of the Balearic Islands. Proyecto final de Investigación, Master en Cambio Global, UIMP-CSIC, Spain.

Marbà, N., Duarte, C.M. (2010) Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. *Global Change Biology* 16: 2366-2375.

Marbà, N., Hemminga, M.A., Mateo, M.A., Duarte, C.M., Mass, Y.E.M., Terrados, J., Gacia, E. (2002) Carbon and nitrogen translocation between seagrass ramets. *Marine Ecology Progress Series* 226: 287-300.

Martín Prieto, J.Á., Roig Munar, F.X., Rodríguez Perea, A., Pons Buades, X., Mir Gual, M., Gelabert Ferrer, B. (2018) Analysis of historic coastline evolution of Es Trenc beach (South of Mallorca): Causes and consequences Análisis de la evolución histórica de la línea de costa de la playa de Es Trenc (S. de Mallorca): causas y consecuencias. *International Review of Geographical Information Science and Technology* 21: 187-214 (in Spanish).

Mascart, T., De Troch, M., Remy, F., Loic, N. M., Lepoint, G. (2018) Seasonal dependence on seagrass detritus and trophic niche partitioning in four copepod eco-morphotypes. *Food Webs* 16(e00086): 1-12.

Mateo, M.A., Romero, J. 1997. Detritus dynamics in the seagrass *Posidonia oceanica*: Elements for an ecosystem carbon and nutrient budget. *Marine Ecology Progress Series* 151: 43-53.

Mateo, M.A., Renom, P., Michener, R.H. (2010) Long-term stability in the production of a NW Mediterranean *Posidonia oceanica* (L.) Delile meadow. *Palaeogeography, Palaeoclimatology, Palaeoecology* 291: 286-296.

Mateo, M.A., Romero, J., Pérez, M., Littler, M.M., Littler, D.S. (1997) Dynamics of millenary organic deposits resulting from the growth of the Mediterranean seagrass *Posidonia oceanica. Estuarine, Coastal and Shelf Science* 44: 103-110.

Mateo-Ramírez, Á., Marina, P., Martín-Arjona, A., Bañares-España, E., García Raso, J.E., Rueda, J.L., Urra, J. (2023) *Posidonia oceanica* (L.) Delile at its westernmost biogeographical limit (Northwestern Alboran Sea): meadow features and plant phenology. *Oceans* 4: 27-48.

Mazzella, L., Scipione, M.B., Gambi, M.C., Buia, M.C., Lorenti, M., Zupo, V., Cancemi, G. (1993) The Mediterranean seagrass *Posidonia oceanica* and *Cymodocea nodosa*. A comparative overview. In: Proceedings of the First International Conference of the Mediterranean coastal Environment, (ed., E. Özhan), pp. 103-116.

Meinesz, A., Cirik, Ş., Akcali, B., Javel, F., Migliaccio, M., Thibaut, T., Yüksek, A., Procaccini, G. (2009) *Posidonia oceanica* in the Marmara Sea. *Aquatic Botany* 90: 18-22.

Meinesz, A., Lefévre, J.R., Astier, J.M. (1991) Impact of coastal development on the infralittoral zone along the southern Mediterranean shore of continental France. *Marine Pollution Bulletin* 23: 343-347.

Menéndez, M., Hernandez, O., Comin, F.A. (2002) Spatial distribution and ecophysiological characteristics of macrophytes in a Mediterranean coastal lagoon. *Estuarine, Coastal and Shelf Science* 55: 403-413.

Migliaccio, M., De Martino, F., Silvestre, F., Procaccini, G. (2005) Meadow-scale genetic structure in *Posidonia oceanica. Marine Ecology Progress. Series* 304: 55-65.

Mohr, W., Lehnen, N., Ahmerkamp, S., Marchant, H.K., Graf, J.S., Tschitschko, B., Yilmaz, P., Littmann, S., Gruber-Vodicka, H., Leisch, N., Weber, M., Lott, C., Schubert, C.J., Milucka, J., Kuypers, M.M.M. (2021) Terrestrial-type nitrogen-fixing symbiosis between seagrass and a marine bacterium. *Nature* 600: 105-109.

Molinier, R., Picard, J. (1952) Recherches sur les herbiers de Phanérogames marines du littoral méditerranéen français. *Annales de l'Institut Océanographique* 27(3): 157-234.

Monnier, B., Lapaquellerie, J., Boudouresque, C.F., Cantaloube, F., Mateo, M.Á., Clabaut, P., Pergent, G., Pergent-Martini, C. (2019) The *Posidonia oceanica* matte: A reservoir of environmental information. In: Proceedings of the Fourteenth International MEDCOAST Congress on Coastal and Marine Sciences, Engineering, Management and Conservation. MECOAST 2019, 22-26 October 2019, Marmaris, Turkey, (ed., Özhan E.), pp. 275-286.

Monnier, B., Pergent, G., Mateo, M.Á., Clabaut, P., Pergent-Martini, C. (2022) Quantification of blue carbon stocks associated with *Posidonia oceanica* seagrass meadows in Corsica (NW Mediterranean). *Science of the Total Environment* 838(155864): 1-14.

Monnier, B., Pergent, G., Valette-Sansevin, A., Boudouresque, C. F., Mateo, M. A., Pergent-Martini, C. (2020) The *Posidonia oceanica* matte: A unique coastal carbon sink for climate change mitigation and implications for management. *Vie et Milieu/Life & Environment* 70(3-4): 17-24.

Montefalcone, M., Albertelli, G., Morri, C., Bianchi, C.N. (2007) Urban seagrass: Status of *Posidonia oceanica* facing Genoa city waterfront (Italy) and implications for management. *Marine Pollution Bulletin* 54: 206-213.

Montefalcone, M., Albertelli, G., Morri, C., Parravicini, V., Bianchi, C.N. (2009) Legal protection is not enough: *Posidonia oceanica* meadows in marine protected areas are not healthier than those in unprotected areas of the northwest Mediterranean Sea. *Marine Pollution Bulletin* 58: 515-519.

Montefalcone, M., Bianchi, C.N., Morri, C., Peirano, A., Albertelli, G. (2006) Lower limit typology and functioning of six *Posidonia oceanica* meadows in the Ligurian Sea (NW Mediterranean). *Biologia Marina Mediterranea* 13(4): 262-266.

Olesen, B., Enríquez, S., Duarte, C.M., Sand-Jensen, K. (2002) Depth-acclimation of photosynthesis, morphology and demography of *Posidonia oceanica* and *Cymodocea nodosa* in the Spanish Mediterranean Sea. *Marine Ecology Progress Series* 236: 89-97.

Orth, R.J., Carruthers, T.J.B., Dennison, W.B., Duarte, C.M., Fourqurean, J.W., Heck, Jr K.L., Hughes, A.R., Hendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L. (2006) A global crisis for seagrass ecosystems. *BioScience* 56 (12): 987-996.

Otero, M.M., Simeone, S., Aljinovic, B., Salomidi, M., Mossone, P., Gerakaris, V., Giunta Fornasin, M.E., Milano, P., Heurtefeux, H., Issaris, Y., Guido, M., Adamopoulou, M. (2018) POSBEMED: Governance and Management of Posidonia Beach/Dune Systems. Final report. IUCN publ., Málaga, Spain: 1-66 + Annexes (in French).

Otero, M.M., Simeone, S., Lindqvist, E., Agaoglou, C., Palombo, L., Hadjioannou, L., Savvides, P., Petrou, N. (2022) A Manual for Conserving Mediterranean Beaches with *Posidonia oceanica* and Assessing Progress of Management Actions. POSBEMED2 Interreg Med Project, IUCN publ., Málaga, Spain.

Oudin, S., Boudouresque, C.F. (2023) Let's preserve the Mediterranean identity of our beaches! Charter of Commitment for beaches with *Posidonia oceanica* banquettes. *Scientific Reports of Port-Cros National Park* 37: 313-334.

Öz, M.I., Yağli, H., Ak, I. (2014) Preliminary study on the distribution of *Posidonia oceanica* along the Dardanelle Strait. In: Proceedings of the 5th Mediterranean Symposium on Marine Vegetation, Portorož, Slovenia, 27-28 October 2014, (eds., Langar, H., Bouafif, C., Ouerghi, A.), RAC/SPA publ., Tunis, pp. 125-130.

Pasqualini, V. (2005) Response of coastal ecosystems to environmental parameters. Mémoire Habilitation à Diriger des Recherches, Biologie des populations et écologie, University of Corsica, Corte (in French).

Patriquin, D.G. (1972) The origin of nitrogen and phosphorus for growth of the marine Angiosperm *Thalassia testudinum. Marine Biology* 15: 35-46.

Peirano, A., Niccolai, I., Mauro, R., Bianchi, C.N. (2001) Seasonal grazing and food preference of herbivores in a *Posidonia oceanica* meadow. *Scientia Marina* 65(4): 367-374.

Pérès, J.M., Picard, J. (1964) New handbook of benthic bionomy of the Mediterranean Sea. *Recueil des Travaux de la Station Marine d'Endoume* 31(47): 3-137 (in French).

Pergent, G., Barralon, E., Monnier, B., Pergent-Martini, C., Valette-Sansevin, A. (2019) Strategy to study blue Carbon ecosystems in Corsica. In: Proceedings of the 6th Mediterranean Symposium on Marine Vegetation, Antalya, Turkey, 14-15 January 2019, (eds., Langar H., Ouerghi A.), RAC/SPA publ., Tunis, pp. 15-20.

Pergent, G., Bazairi, H., Bianchi, C.N., Boudouresque, C.F., Buia, M.C., Clabaut, P., Harmelin-Vivien, M., Mateo, M.A., Montefalcone, M., Morri, C., Orfanidis, S., Pergent-Martini, C., Semroud, R., Serrano, O., Verlaque, M. (2012) Mediterranean Seagrass Meadows: Resilience and Contribution to Climate Change Mitigation. A Short Summary. IUCN publ., Gland, Málaga.

Pergent, G., Romero, J., Pergent-Martini, C., Mateo, M.A., Boudouresque, C.F. (1994) Primary production, stocks and fluxes in the Mediterranean seagrass *Posidonia oceanica. Marine Ecology Progress Series* 106: 139-146.

Pergent, G., Semroud, R., Baba Ahmed, R., Delbal, F., Khatal, Y., Remili, A., Robert, P., Boudouresque, C.F. (1993) Preliminary data on the distribution and state of the *Posidonia oceanica* seagrass meadow in the El Kala region (Algeria). *Scientific Reports of Port-Cros National Park* 15: 253-263 (in French).

Pergent-Martini, C., Bonacorsi, M., Clabaut, P., Pasqualini, V., Pergent, G. (2013) Regression of *Posidonia oceanica* meadow: fact or fiction? *Rapports de la Comission. Internationale de la Mer Méditerranée* 40: 680.

Pergent-Martini, C., Pergent, G., Fernandez, C., Ferrat, L. (1999) Value and use of *Posidonia oceanica* as a biological indicator. *EMECS Joint Conference, Medcoast* 99: 73-89.

Personnic, S., Boudouresque, C.F., Astruch, P., Ballesteros, E., Blouet, S., Bellan-Santini, D., Bonhomme, P., Thibault-Botha, D., Feunteun, E., Harmelin-Vivien, M., Pergent, G., Pergent-Martini, C., Pastor, J., Poggiale, J.C., Renaud, F., Thibaut, T., Ruitton, S. (2014) An ecosystem-based approach to assess the status of a Mediterranean ecosystem, the *Posidonia oceanica* seagrass meadow. *Plos OnE* 9(6, e98994): 1-17.

Piñeiro-Juncal, N., Leiva-Dueña,s C., Serrano, O., Mateo, M.A., Martínez-Cortízas, A. (2020) Pedogenic processes in a *Posidonia oceanica* mat. *Soil Systems* 4(18): 1-15.

Por, F.D. (2009) Tethys returns to the Mediterranean: Success and limits of tropical re-colonization. *BioRisk* 3: 5-19.

Poulos, S.E., Collins, M.B. (2002) Fluviatile Sediment Fluxes to the Mediterranean Sea: A Quantitative Approach and the Influence of Dams. In: Sediment Fluxes to Basins: Causes, Controls and Consequences, (eds., Jones, S.E., Frostick, L.E.), Geological Society, London, 191, pp. 227-245.

Prado, P., Tomas, F., Alcoverro, T., Romero, J. (2007) Extensive direct measurements of *Posidonia oceanica* defoliation confirm the importance of herbivory in temperate seagrass meadows. *Marine Ecology Progress Series* 340: 63-71.

Pregnall, A.M., Smith, R.D., Kursar, T.A., Alberte, R.S. (1984) Metabolic adaptation of *Zostera marina* (eelgrass) to diurnal periods of root anoxia. *Marine Biology* 83: 141-147.

Provansal, M., Sabatier, F., Raccasi, G., Maillet, G., Antonelli, C., Fleury, J. (2009) Sedimentary Inputs from the Rhône to the Sea. Secular Variability and Impacts of Development Projects. In: Le Golfe du Lion. Un observatoire de l'environnement en Méditerranée, (eds., Monaco, A., Ludwig, W., Provansal, M., Picon, B.), Editions Quae publ., Versailles, pp. 301-313 (in French).

Ramos-Esplá, A.A., Aranda, A., Gras, D., Guillen, J.E. (1994) Impacts on *Posidonia oceanica* (L.) Delile Meadows in SE Spain: Need to Establish Coastal Planning and Management Tolos. In: Pour qui la Méditerranée au 21° siècle?

Villes des rivages et environnement littoral en Méditerranée, Montpellier, pp. 64-69 (in Spanish).

Remy, F., Mascart, T., De Troch, M., Michel, L.N., Lepoint, G. (2018) Seagrass organic matter transfer in *Posidonia oceanica* macrophytodetritus accumulations. *Estuarine, Coastal and Shelf Science* 212: 73-79.

Ricklefs, R.E., Miller, G.L. (2005) Ecology. De Boeck publ., Louvain-la-Neuve, Belgium (in French).

Roig-Munar, F.X., Rodríguez-Perea, A., Martín Prieto, J.Á., Galaber Ferrer, B. (2019) Quantification of sediment loss due to mechanical removal of *Posidonia oceanica* berms (banquettes) on the beaches of the Balearic Islands: Geomorphological consequences. *Revista de la Sociedad Geológica de España* 32(2): 73-86 (in Spanish).

Romero, J. (2004) Seagrass Meadows. Primary Production and Its Fate. Characteristics of Plant Remains. In: Praderas y bosques marinos de Andalucía, (eds., Luque, A.A., Templado, J.), Consejería de Medio Ambiente, Junta de Andalucía publ., Sevilla, Spain, pp. 74-81 (in Spanish).

Romero, J., Perez, M., Alcoverro, T., Mateo, M.A., Sanchez-Lizaso, J.L. (1998) Production ecology of *Posidonia oceanica* (L.) Delile meadows in Nueva Tabarca Marine Reserve: Growth, biomass and nutrient stocks along a bathymetric gradient. *Oecologia Aquatica* 11: 111-121.

Rovere, A., Montefalcone, M., Vassalio, P., Paoli, C., Vacchi, M., Morri, C., Bianchi, C.N., Albertelli, G., Fabiano, M. (2010) *Posidonia oceanica* through time: Modern and paleoecological perspectives from the Bergeggi – Vado Ligure area (SV). *Biologia Marina Mediterranea* 17(1): 157-160.

Scemama, P., Kermagoret, C., Astruch, P., Boudouresque, C.F., Changeux, T., Harmelin-Vivien, M., Ourgaud, M., Ruitton, S., Verlaque, M., Charbonnel, E., Alban, F., Accornero-Picon, A., Le Direac'h, L. (2024) Impact assessment of multiple pressures on ecosystem services with a state and transition model: Application to *Posidonia oceanica* seagrass meadows. *Journal of Environmental Management* 367(121888): 1-13.

Schroeder, K., Chiggiato, J. (eds.) (2023) Oceanography of the Mediterranean Sea. An Introductory Guide. Elsevier, Amsterdam.

Serrano, O., Lavery, P.S., López-Marino, L., Ballesteros, E., Mateo, M.A. (2016) Location and associated carbon storage escarpments of seagrass *Posidonia* mats. *Frontiers in Marine Science* 3(42): 1-7.

Sharaf El Din, S.H. (1977) Effect of the Aswan High Dam on the Nile flood and on the estuarine and coastal circulation pattern along the Mediterranean Egyptian coast. *Limnology and Oceanography* 22(2): 194-207.

Shirinov, S., Federico, I., Bonamano, S., Causio, S., Biocca, N., Piermattei, V., Piazzolla, D., Alessandri, J., Mentaschi, L., Coppini, G., Marcelli, M., Pinardi, N. (2025) Modelling vegetation-induced wave attenuation: The impact of seagrass seasonal variability and biomechanical flexibility. *Natural Hazards and Earth System Science* 25: 3737-3758.

Short, F.T., Dennison, W.C., Capone, D.G. (1990) Phosphorus limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. *Marine Ecology Progress Series* 62: 169-174.

Sierra, J.P., Gracia, V., Castell, X., García-León, M., Mösso, C., Lin-Ye, J. (2023) Potential of transplanted seagrass meadows on wave attenuation in a fetch-limited environment. *Journal of Marine Science and Engineering* 11(1186).

Simeone, S., De Falco, G. (2013) *Posidonia oceanica* banquettes removal: Sedimentological, geomorphological and ecological implications. *Journal of Coastal Research* special issue 65: 1045-1050.

Simeone, S., Molinaroli, E., Conforti, A., De Falco, G. (2018) Impact of ocean acidification on the carbonate sediment budget of a temperate mixed beach. *Climatic Change* 150: 227-242.

Spalding, M., Taylor, M., Ravilious, C., Short, F., Green, E. (2003) The Distribution and Status of Seagrasses. In: World Atlas of Seagrasses, (eds., Green, E.P., Short, F.T.), University of California Press publ., Berkeley, pp. 5-26.

Syvitski, J.M.P., Vörömarty, C.J., Kettner, A.J., Green, P. (2005) Impact of humans on the flux of terrestrial sediments to the global coastal ocean. *Science* 308: 376-380.

Taviani, M. (2002) The Mediterranean benthos from late Miocene up to present: Ten million years of dramatic climatic and geologic vicissitudes. *Biology Marine Mediterranea* 9(1): 445-463.

Telesca, L., Belluscio, A., Criscoli, A., Ardizzone, G., Apostolaki, E.T., Fraschetti, S., Gristina, M., Knittweis, L., Martin, C.S., Pergent, G., Alagna, A., Badalamenti, F., Garofalo, G., Gerakaris, V., Pace, M.L., Pergent-Martini, C., Salomidi, M. (2015) Seagrass meadows (*Posidonia oceanica*) distribution and trajectories of change. *Scientific Reports* 5(12505): 1-14.

Templado, J. (1984) *Posidonia oceanica* Meadows in Southeastern Spain and Their Biocenosis. In: International Workshop on *Posidonia oceanica* Beds, (eds., Boudouresque, C.F., Jeudy de Grissac, A., Olivier, J.), GIS Posidonie publ., Marseille, pp. 159-172 (in Spanish).

Templado, J., Ballesteros, E., Garcia-Raso, J.E., San Martin, G., Lopez-Garcia, E., Salas, C., Luque, A.A., Sanchez-Lizaso, J.L., Moreno, D. (2004) Seagrass Meadows. The *Posidonia* Community. In: Praderas y bosques marinos de Andalucía, (eds., Luque, A.A., Templado), Consejería de Medio Ambiente, Junta de Andalucía publ., Sevilla, Spain, pp. 89-116 (in Spanish).

Thibaut, T, Blanfuné, A, Boudouresque, C.F., Personnic, S., Ruitton, R., Ballesteros, E., Bellan-Santini, D., Bianchi, C.N., Bussotti, S., Cebrian, E., Cheminée, A., Culioli, J.M., Derrien-Courtel, S., Guidetti, P., Harmelin-Vivien, M., Hereu, B., Morri, C., Poggiale, J.C., Verlaque, M. (2017) An ecosystem-based approach to assess the status of Mediterranean algae-dominated shallow rocky reefs. *Marine Pollution Bulletin* 117: 311-329.

Tomasello, A., Borruso, A., Calì, P., Cascino, F., Di Maida, G., Pirrota, M., Calvo, S. (2001) Analysis of the bathymetric distribution of the lower limit of the *Posidonia oceanica* (Linnaeus) Delile meadows along the Sicilian Coasts. In: *Posidonia oceanica* Meadows, Conservation and Experiences, Proceedings of the Workshop held in Le Castella on 1 December 2001, (ed., Infantino E.), A.M.P. Capo Rizzuto publ., Crotone, Italy, pp. 133-137 (in Italian).

Traganos, D., Lee, C.B., Blume, A., Poursanidis, D., Čižmek, H., Deter, J., Mačić, V., Montefalcone, M., Pergent, G., Pergent-Martini, C., Ricart, A.M., Reinartz, P. (2022) Spatially explicit seagrass extent mapping across the entire Mediterranean. *Frontiers in Marine Science* 9(871799): 1-13.

Vacchi, M., Ghilardi, M., Spada, G., Currás, A., Robresco, S. (2017) New insights into the sea-level evolution in Corsica (NW Mediterranean) since the late Neolithic. *Journal of Archaeological Science: Reports* 12: 782-793.

Valiela I. (1991) Ecology of Coastal Ecosystems. In: Fundamentals of Aquatic Ecology., (eds., Barnes, R.S.K., Mann, K.H.), Blackwell Scientific Publications, Oxford, pp. 57-76.

Vandarakis, D., Kourliaftis, I., Salomidi, M., Gerakaris, V., Issaris, Y., Agaoglou, Ch., Kapsimalis, V., Panagiotopoulos, I. (2022) Geomormological Approaches to Study *Posidonia* Banquettes and Their Effects on the Coastal Front of Schinias-Marathon National Park. In: Monitoring of Mediterranean Coastal Areas: Problems and Measurement Techniques, Livorno (Italy), Ninth International Symposium, (eds., Bonora, L., Carboni, D., De Vincenzi, M., Matteucci, G.), Firenze University Press, Firenze, Italy, pp. 93-103.

Vassallo, P., Paoli, C., Rovere, A., Montefalcone, M., Morri, C., Bianchi, C.N. (2013) The value of the seagrass *Posidonia oceanica*: A natural capital assessment. *Marine Pollution Bulletin* 75(1-2): 157-167.

Velimirov, B. (1984) DOC in the water column above *Posidonia* meadows. In: International Workshop on *Posidonia oceanica* Beds, (eds., Boudouresque, C.F., Jeudy de Grissac, A., Olivier, J.), GIS Posidonie publ., Marseille, France, pp. 179-184.

Velimirov, B. (1986) DOC dynamics in a Mediterranean seagrass system. *Marine Ecology Progress Series* 28: 21-41.

Verlaque, M., Nedelec, H. (1983) Biology of *Paracentrotus lividus* (Lamarck) on rocky substrate in Corsica (Mediterranean, France): diet of adults. *Vie et Milieu* 33(3-4): 191-201.

Vizzini, S. (2009) Analysis of the trophic role of Mediterranean seagrasses in marine coastal ecosystems: A review. *Botanica Marina* 52(5): 383-393.

Vizzini, S., Sarà, G., Mateo, M.A., Mazzola, A. (2003) $\delta\ ^{13}C$ and $\delta\ ^{15}N$ variability in *Posidonia oceanica* associated with seasonality and plant fraction. *Aquatic Botany* 76: 195-202.

Vohník, M., Borovec, O., Kolařík, M. (2016) Communities of cultivable root mycobionts of the seagrass *Posidonia oceanica* in the northwest Mediterranean Sea are dominated by a hitherto undescribed pleosporalean dark septate endophyte. *Microbial Ecology* 71: 442-451.

Vohník, M., Borovec, O., Kolaříková, Z., Sudová, R., Réblová, M. (2019) Extensive sampling and high-throughput sequencing reveal *Posidoniomyces atricolor* gen. et sp. nov. (Aigialaceae, Pleosporales) as a dominant root mycobiont of the dominant Mediterranean seagrass *Posidonia oceanica. MycoKeys* 44: 59-86.

Vohník, M., Borovec, O., Župan, I., Kolařík, M., Sudová, R. (2017) Fungal root symbionts of the seagrass *Posidonia oceanica* in the central Adriatic Sea revealed by microscopy, culturing and 454-pyrosequencing. *Marine Ecology Progress Series* 583: 107-120.

Vohník, M., Borovec, O., Župan, I., Vondrášek, D., Petrtýl, M., Sudová, R. (2015) Anatomically and morphologically unique dark septate endophytic association in the roots of the Mediterranean endemic seagrass *Posidonia oceanica. Mycorrhiza* 25(8): 663-672.

Vu, M.T. (2018) A Digital Approach for the Design of Coastal Protection Structures on the Eastern Tombolo of the Giens Peninsula. Doctoral thesis, University of Toulon, France (in French).

Wainwright, B.J., Zahn, G.L., Zushi, J., Lee, N.L.Y., Ooi, J.L.S., Lee, J.N., Huang, D. (2019) Seagrass-associated fungal communities show distance decay of similarity that has implications for seagrass management and restoration. *Ecology and Evolution* 9(19): 11288-11297.