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Abstract

Here we review the multiple interactions between the endemic Mediterranean seagrass, *Posidonia oceanica*, and coastal geomorphologic processes as an outstanding example of biogeomorphology, taking into account recent advances in the field. Seagrass meadows are among the most important elements for the functioning of marine coastal ecosystems, and represent a major focus for research and conservation. Being considered a priority habitat, *P. oceanica* meadows are protected by several EU directives and national laws. In this state of science paper we examine: the role of sedimentary features in controlling the development of the meadows; the interplay between *P. oceanica* leaf litter (i.e. beached necromass) cast ashore and erosional-depositional processes on the beaches; the interactions between meadows and nearshore hydrodynamics, and; possible linkages between geomorphological features of the seafloor and the architecture of meadows. Finally, we provide perspectives for future research on *P. oceanica* and other Mediterranean seagrass meadows in a biogeomorphological context with specific reference to climate change.

Keywords: *Posidonia oceanica*; Biogeomorphology; Coastal Ecosystems; Coastal Processes; Mediterranean Sea.

1. Introduction

Seagrass meadows are among the most important elements for the functioning of marine coastal ecosystems, and represent a major focus for research and conservation (Koch et al., 2006; Short et al., 2011). However,

the combined effects of both anthropogenic and natural disturbances is leading to a global decline of seagrass meadows, with rates of loss estimated at 2–5% per year (Waycott et al., 2009; Short et al., 2011). Identifying the causes of this worldwide decline in order to ultimately protect these important coastal elements is a priority task (Green and Short, 2003). As a consequence, extensive research in the last few decades has investigated the factors, either natural or human, controlling the distribution of seagrasses in the coastal environment. Importantly, investigation of the multiple interactions between ecological and geomorphological processes (i.e., biogeomorphology) can contribute to define how terrestrial, transitional and marine systems respond to disturbances (Burnett et al., 1998; Naylor et al., 2002; Viles et al., 2008).

The role of geomorphological factors in influencing the spatial and temporal patterns of vegetation in different terrestrial, transitional and marine environments has proved a mainstay of biogeomorphological research (e.g., Howard and Mitchell, 1985; Viles, 1988; Corenblit et al., 2007), but whilst in the terrestrial environment the relationships between vegetation and geomorphology are relatively well-known, such relationships have been comparatively less investigated in the marine environment (Guidetti et al., 2004; Coombes et al., 2013).

This paper reviews the complex interplay between the endemic species *Posidonia oceanica* (Linnaeus) Delile, the most important and abundant seagrass in the Mediterranean Sea, and the littoral system.

P. oceanica meadows form a key coastal habitat playing a crucial role in the physical equilibrium of a large portion of the Mediterranean coasts (Boudouresque et al., 2012): they attenuate waves and currents, reduce sediment resuspension, protect the beach from erosion, and contribute to shoreline stabilization (e.g. Boudouresque and Jeudy de Grissac, 1983; Gacia and Duarte, 2001; Boudouresque et al., 2012).

1.1. *Posidonia oceanica* meadow distribution

Posidonia oceanica meadows cover about 1.5% of the total Mediterranean Sea surface (Pasqualini et al., 1998) and occur in 16 Mediterranean countries (e.g. Giakoumi et al., 2012; Figure 1). Meadows are less abundant in the Levantine Sea, whilst sparse occurrence and even complete absence of *P. oceanica* meadows are reported in the Marmara Sea and in Black Sea, respectively (Boudouresque et al., 2012; Figure 1). Along the western Mediterranean basin, *P. oceanica* meadows are widespread, but because of low salinity values and/or climate, they are rare or absent in the Northern Adriatic Sea (Gamulin-Brida, 1974) and along the

Languedoc coast (Southern France) between the Rhone delta and Port la Nouvelle (Boudouresque and Meinesz, 1982). At about 250 km east of the Gibraltar strait, the complex mixing of different density waters between the Atlantic Ocean and the Mediterranean Sea (known as the Almeria–Oran front) represents the western boundary of *P. oceanica* distribution (Marbà et al., 1996; Gobert et al., 2006; Giakoumi et al., 2012).

1.2. *Posidonia oceanica* meadow structure and dynamics

Posidonia oceanica meadows are usually recorded from near the surface to 40 m depth (Boudouresque and Meinesz, 1982; Gobert et al., 2006; Boudouresque et al., 2012), but living plants have been found as deep as 48 m in particularly clear waters (Boudouresque et al., 2012). *P. oceanica* meadow architecture can exhibit continuous cover of the seabed or be organised in patches of various shapes, including strips parallel to the shoreline or cordons perpendicular to the shoreline (Borg et al., 2005; Boudouresque et al., 2012). Depth and nature of the upper (landward) and lower (seaward) limits are other important parameters characterising meadow architecture (Montefalcone, 2009). Limit typology allows the limiting factors to be inferred: light attenuation causes a shaded limit, change in substratum characteristics (e.g., from sand to mud) a sharp limit, occurrence of bottom currents an eroded limit. Regressed limits can be recognised by their depth (shallower than expected in normal conditions) and by the occurrence of dead 'matte' (see section 2 for 'matte' definition) beyond the present limit (Table 1). Regressive aspects of the upper limit have also been described, with meadow fragmentation mostly resulting from human impacts (Montefalcone et al., 2010). In favourable conditions, the most relevant feature of the upper limit is the occurrence of extremely shallow formations in calm water, with leaves reaching and spreading out on the sea surface (Augier and Boudouresque, 1970).

The linkage between seagrass meadow development and sedimentary features of the seafloor has been the focus of several studies (e.g., Fonseca, 1996; Madsen et al., 2001; De Falco et al., 2003; Boudouresque et al., 2012). However, recent investigations have demonstrated that sedimentary features alone are poor determinants of marine species distribution (Hemer, 2006; Post et al., 2006; Ryan et al., 2007). In shallow underwater environments, local geomorphology, currents and wave exposure play a very significant role in controlling habitat distribution, particularly for seagrass meadows (Short et al., 2002; Koch et al., 2006; Ryan et al., 2007).

In this state of science paper we explore different aspects of *P. oceanica* meadows at the interface between geology, geomorphology and ecology, taking into account recent advances in this field. Specifically we discuss: (i) the role of sedimentary features in controlling the development of seagrass meadows (section 2); (ii) the interplay between *P. oceanica* leaf litter cast ashore (i.e. beached necromass) and beach erosional-depositional processes (section 3); (iii) the interactions between meadow and nearshore hydrodynamics (section 4) and; (iv) possible linkages between geomorphological features of the seafloor and the architecture of meadows, based on ongoing research (section 5). Finally, we consider perspectives for future biogeomorphological research on Mediterranean seagrass meadows (section 6).

2. Sediments and *Posidonia oceanica* meadow development

The growth dynamics of *Posidonia oceanica* meadows and sedimentary processes are linked by complex feedback relationships (de Boer, 2007), which have been qualitatively observed since the 1980s (Boudouresque and Jeudy de Grissac, 1983). The plant is capable of adapting its growth rate and inclination of its rhizome branches to the rate of sediment deposition. Rhizomes can grow either vertically or horizontally, thus showing erect (orthotropic) or prostrate (plagiotropic). The orthotropic rhizomes mainly develop in crowded situations, whereas the plagiotropic rhizomes are more typical of areas undergoing colonisation (for instance, at the borders of clearings). Progressive silting and the alternation of the two types of rhizome growth result in a typical terraced formation called 'matte', consisting of interlaced remnants of roots, rhizomes and entangled sediment (Giovannetti et al., 2008). More than an analogue of terrestrial soil vegetation, the matte may also be considered a form of bioconstruction (Bianchi, 2001).

Experimental observations based on sediment traps have highlighted that *P. oceanica* meadows can trap fine particles, thus buffering fine sediment re-suspension (Gacia et al., 1999). This process explains the considerable amount of silt-clay content observed within matte sediments from sites: 50-150 $kg \cdot m^{-3}$ in the Gulf of Oristano (Western Sardinia, Italy: De Falco et al., 2000) and 92.3±4.9 $kg \cdot m^{-3}$ in Port Lligat (Cadaqués, Girona, NW Spain: Serrano et al., 2012). Based on economic assessment, sediment retention and wave attenuation are probably the most valuable ecosystem services provided by *P. oceanica* meadows (Vassallo et al., 2013).

In contrast, if sedimentation rate exceeds a threshold value, meadows can disappear. For this reason, alongside lower salinity, meadows are generally absent from the mouth of coastal rivers, in the areas of fine sediment deposition (Pasqualini et al., 1998; De Falco et al., 2006), due to high sedimentation rates and reduced light associated with increased water turbidity. Smothering of plants due to changes in sediment dynamics in coastal areas is one of the major threats to the meadows (Lasagna et al., 2006, 2011). Decline of meadows by sedimentation in association with beach nourishments schemes has also been reported in several case studies (Guidetti, 2007; Cabaço et al., 2008; González-Correa et al., 2008). Manzanera et al. (1998) used field manipulations of the sediment input to *P. oceanica* meadows to show that shoot mortality reached 100% after 200-300 days when sediment thickness was 15 cm above the initial level: these figures should not be interpreted as sedimentation rates. The sediments accumulating inside meadows generally show a high percentage of biogenic carbonate particles produced by the biota associated with the seagrass ecosystem, such as coralline algae, foraminifers, gastropods, bivalves, serpulid polychaetes, bryozoans, and echinoids (Fornós and Ahr, 1997). The carbonate sediments associated with *P. oceanica* can be transported inshore, thus affecting the composition of adjacent beach sediments. This was observed in the Balearic Islands (Gomez Pujol et al., 2013), in Western Sardinia (De Falco et al., 2003), and in pocket beaches of Southern Corse (unpublished data). For this reason, *P. oceanica* meadows are considered a major "carbonate factory" of the Mediterranean inner shelf (Canals and Ballesteros, 1997; Fornós and Ahr, 1997, 2006; De Falco et al., 2008a, 2011; Mateu-Vicens et al., 2012). In this respect, current trends in seawater acidification (Bianchi et al., 2012) probably represent a threat to these processes in the Mediterranean Sea (Figure 2).

In comparison with other Mediterranean coastal benthic ecosystems, carbonate production in meadows, evaluated by sampling leaf epiphytes only, is low (69-157 $gCaCO_3\ m^{-2}{\cdot}a^{-1}$; e.g., Canals and Ballesteros, 1997). Estimates based on the rhizome growth rate of meadows located in the northern sector of the Gulf of Oristano (western Sardinia, Italy) indicate that carbonate production is in the range of 390–1147 $gCaCO_3\ m^{2}{\cdot}a^{-1}$ (De Falco et al., 2008a). These values are amongst the highest for seagrass ecosystems (Gacia et al., 2003) and lay within the range calculated for coral reefs (Bianchi, 2001). The discrepancy between estimates of carbonate production is likely methodological, given that carbonate particles contained in calcified epiphytes do not account for the contribution of shells and tests of the motile fauna associated with the meadow.

Very high-resolution seismic surveys at Port Lligat (Cadaqués, Girona, NW Spain) revealed that matte thickness over the primary substrate ranged from 4.3 to 11.7 m (Lo Iacono et al., 2008). Matte coring in the same sites enabled inorganic sediment (skeletal carbonates plus fine sediments) accumulation rates to be estimated, as well as for organic particles over a period spanning about 5000 years (Serrano et al., 2012): inorganic sediment deposition was estimated at 898.6±26.3 $g_{DW} \cdot m^{-2} \cdot a^{-1}$, including 120.0±6.4 $g_{DW} \cdot m^{-2} \cdot a^{-1}$ mud fraction (<63 μm); organic skeletal carbonate was estimated at 452.9±15.5 $g_{DW}CaCO_3 \cdot m^{-2} \cdot a^{-1}$. These values agree well with those estimated for western Sardinia (De Falco et al., 2000, 2008a). The sediments below *P. oceanica* meadows meet requirements to be considered a soil, classified as Limnic Subaquatic Histosols (Calcaric, Eutric) (Serrano et al., 2012). The sedimentary facies observed in association to *P. oceanica* meadows, composed of carbonate skeletal sand mixed with a variable amount of siliciclastic sand and silt-clay fractions, have also been considered analogues for interpreting the occurrence and importance of these types of deposits in the rock record (Pomar et al., 2004).

In contrast, *P. oceanica* meadows also colonise sediments of terrestrial origin (see for instance Cavazza et al., 2000; De Falco et al., 2008a) and rocky substrates (De Falco et al., 2003). The sedimentary depositional environment seems influenced by the spatial distribution of wave energy. For instance, biogenic carbonate reefs associated with *P. oceanica* meadows develop in sheltered areas characterised by low wave amplitude. In the exposed locations, meadows colonise relict siliciclastic sediments or rocky substrate, with a lower rate of carbonate particle deposition (De Falco et al., 2008a, 2011) and an absence of thick matte development. In western Sardinia, De Falco et al. (2008a) found that *P. oceanica* in sheltered areas exhibits higher rhizome growth rates (associated with biogenic sedimentary facies) compared to exposed areas (1.1-1.2 $cm \cdot a^{-1}$ and 0.7 $cm \cdot a^{-1}$, respectively) and a lower percentage of horizontal shoots (1.1-4.1% vs. 18%, respectively). Here, sheltered meadows tended to develop in a vertical direction, thus contrasting the sediment deposition rate. Meadows in exposed locations tended to expand laterally due to the absence of sediment deposition (De Falco et al., 2008a). Nevertheless, relationships between meadow growth dynamics and sedimentary processes still need to be clarified using further comparison of substrate characteristics and wave hydrodynamics for a larger number of case studies.

3. *Posidonia oceanica* leaf litter and beach morphodynamics

Seagrass beach-cast leaf litter deposits (i.e. beached necromass *sensu* Boudouresque et al., 2015) are common in many coastal areas around the world (De Falco et al., 2008b; Mossbauer et al., 2012; Gomez-Pujol et al., 2013). This organic material can occur in large amounts and can play a role in the geomorphic evolution of beaches under normal wave conditions (i.e., not under storm conditions), in particular on low energy beaches (Jackson et al., 2002). Short (1999) used the term 'seagrass berm' to describe leaf litter deposited on beaches along the Australian coastline, but in the Mediterranean the French term ‘banquette’ is most widely used (Boudouresque et al., 2015).

Banquettes are wedge-shaped structures, which range from a few centimetres to several metres thick. Similarly to sediment berms, banquettes can be considered features resulting from the accumulation of seagrass necromass (leaves and rhizomes) and sediments at the extreme landward point of wave influence (Simeone and De Falco, 2012).

Formation of seagrass berm deposits depends on the availability of leaf litter on the upper shoreface (Simeone and De Falco, 2012; Gomez-Pujol et al., 2013). *P. oceanica* sheds leaves mostly in late summer and autumn (Mateo and Romero, 1996), and the leaf litter can be found along sandy shores (De Falco et al., 2008b). On sheltered beaches (Figure 3a), the presence of leaf litter on submerged beaches is related to the proximity of *P. oceanica* meadows to the shoreline, as for other seagrasses and terrestrial plant species colonising the foreshore (Jackson et al., 2002; Simeone and De Falco, 2012). On exposed beaches (Figure 3b), leaf litter can be transported as floating material during storms and can be deposited, when the storm decreases in energy, far from the meadow from which the leaf litter originates (Simeone and De Falco, 2012). On embayed beaches, leaf litter deposited on the seafloor can remain enclosed by headlands for a long period of time (from days to seasons), and this can promote repeated cycles of deposition and erosion of seagrass berms on this beach typology (Simeone et al., 2013a,b).

In this respect, beach-cast leaf litter is part of the material exchanged among submerged beach section, the emerged beach and dunes. On high-energy shores, *P. oceanica* banquettes are located along the beach-face (berm area), where high beach surface variability occurs (Simeone and De Falco, 2012). This variability is primarily due to sediment deposition and, secondly, to the deposition and erosion of leaf litter. On the other hand, for low energy beaches (*sensu* Jackson et al., 2002), seagrass berm erosion and growth is mainly

driven by the exchange of organic leaf litter between the beach-face and the shore-face, whilst the sedimentary substrate is quite immobile (Simeone and De Falco, 2012).

Mateo et al. (2003) proposed a sequence of formation and destruction of banquettes. This involves an initial stage of leaf litter deposition, leading to berm accretion up to the maximum height (2.2 m in the case studied). Erosion due to wave action, acting at the base of the banquette, leads to scarp formation and the collapse of the berm structure (Mateo et al., 2003). The morphology and composition of seagrass berms highlight that the deposition of leaf litter on beaches starts landward, where heavier material settles (i.e., rhizomes, if present, and mineral grains) and proceeds seaward, where leaves become predominant when storm energy decreases (Simeone and De Falco, 2012). This pattern of litter berm development is confirmed for *P. oceanica* based on remote sensing (camera and video) of several cycles of deposition and erosion during storms on different Mediterranean beaches (Gomez-Pujol et al., 2013; Simeone et al., 2013a).

P. oceanica banquettes characterising Mediterranean beaches likely play a role in the exchange of material between beach and foredune, as for other beach litter deposits (Nordstrom et al., 2011) and for other species of seagrass (Hemminga and Nieuwenhuize, 1990). Field observations from the western coast of Sardinia have shown that, in some cases, foredune systems are constituted of alternating layers of *P. oceanica* leaves and sediment (De Falco et al., 2003). In addition, leaves and fragments of *P. oceanica* transported inland by winds and trapped by pioneer plants can enhance sand moisture content, favour nutrient uptake by plants (Cardona and Garcia, 2008; Del Vecchio et al., 2013), and thereby can have a positive effect on the accretion of the foredune.

Although banquettes are often suggested to play a role in beach protection from erosion (Boudouresque and Jeudy De Grissac, 1983; Mateo et al., 2003), very few studies have been published on this issue. On low energy and short fetch beaches, beach-cast leaf litter can resist waves and be effective in suppressing wave run-up and limiting beach change (Nordstrom and Jackson, 2012). In contrast, Gomez-Pujol et al. (2013) found that seagrass berms were eroded during swell conditions between two consecutive storms on a semi enclosed beach in the Balearic Islands. Under such conditions, the capacity of these features to protect beach from erosion during storms is thought to be negligible, because no interaction between waves and beach-cast leaf litter can occur. In other Mediterranean regions, the residence time of seagrass berms on beaches is higher than the time interval between storms (Simeone and De Falco, 2012; Simeone et al., 2013a). In these

cases, some proportion of storm energy may be dissipated by the destruction of the banquettes. For example in Sardinia, Simeone and De Falco (2012) found that waves and storms were responsible for reducing beach face leaf litter from more than 9000 m^3 to ~1000 m^3 between February to May.

Beach-cast leaf litter deposits are often removed as part of beach management, often for aesthetic reasons. Several attempts to regulate removal operations have been made at different levels (ISPRA, 2010 at the Italian national level) and alternative management practices have been suggested, such as the utilisation of the beach cast leaf litter in agriculture (www.beachmed.it, www.lifeprime.eu, access date 11/01/2016). This practice, often carried out with heavy machinery, may however have consequent impacts on the beach (De Falco et al., 2008b; Simeone et al., 2013c). Removal could influence the beach morphology, such as flattening the beach profile and obliterating sedimentary features (e.g., sediment berms, cusps, embayments, beach-face steps). Hence, this practice can indirectly affect swash processes, in particular run-up regimes. In addition, removal of seagrass berms from beaches can affect the local sediment budget: data collected in Western Sardinian showed that an average of 60 $kg \cdot m^{-3}$ of sediment can be trapped in seagrass berms (Guala et al., 2006; De Falco et al., 2008a; Simeone et al., 2013a). Berm removal can influence the sediment budget most significantly when it is performed on small embayed beaches composed of relict sediment, which is common for the beaches of the western coast of Sardinia (Bird, 2008; Simeone et al., 2013b).

The debate on the protection from erosion afforded by seagrass berms remains unresolved. In particular, in terms of wave modification more studies are needed on the interactions between waves approaching the beach and the *P. oceanica* leaf litter derived from the destruction of banquettes during storm events.

4. *Posidonia oceanica* and nearshore hydrodynamics

The major role of seagrass meadows in terms of wave attenuation and modification of local hydrodynamics has already been underlined by Fonseca and Cahalan (1992). Hydrodynamic attenuation, together with sediment retention, has also been recognised as a major ecosystem service provided by *P. oceanica* meadows (Vassallo et al., 2013), as it leads to an effective protection from shoreline erosion. These processes have been intensively investigated in the last decade using flume laboratory experiments (e.g., Folkard, 2005; Sánchez-González et al., 2011; Stratigaki et al., 2011; Manca et al., 2012), field measurements (e.g., Basterretxea et al., 2004; Infantes et al., 2009, 2012; Vacchi et al., 2010, 2012), or a combination of both

(e.g., Infantes et al., 2011; Beachmed-e, subproject NAUSICAA,http://www.beachmed.it/Beachmede/SousProjets/NAUSICAA/tabid/87/Default.aspx, access date 11/01/2016). Meadows dampen swell and form an obstacle to the movement of sediments on the bed reducing hydrodynamic forces of waves and bottom currents (Boudouresque et al., 2012, and references therein). Early studies showed that hydrodynamic forces are reduced between 10% and 75% under the leaves (Gacia et al., 1999), and by 20% a few centimetres over the meadows (Gacia and Duarte, 2001). This attenuation actively reduces littoral erosion (Boudouresque et al., 2012). Similar effects of wave attenuation have also been reported for other marine coastal habitats, such as kelp forests (Kobayashi, 1993, and references therein), tidal marshes (Neumeier and Ciavola, 2004; Möller et al., 2014) and coral reefs (Hardy and Young, 1996; Ferrario et al., 2014 and references therein).

Many of the above mentioned studies have significantly improved our understanding of the interplay between seagrass meadows and hydrodynamics by investigating the influence of wave energy on the establishment, growth, and maintenance of *P. oceanica*, as well as providing quantitative models to predict the evolution of meadows as a function of hydrodynamics.

4.1. Influence of meadows on nearshore hydrodynamics

P. oceanica meadows usually occur within the most dynamic region of the seafloor (Boudouresque et al., 2012), strongly influenced by waves and currents. Referring to low-energy beaches, Basterretxea et al. (2004) suggested that meadows influence the relative stability of the beach by controlling the local morphodynamic domain (i.e., the distinctive type of beach produced by the topography, wave climate and sediment composition) and by constraining sediment transport. Only during episodic storm events, when nearshore energy is increased, is energy supply sufficient to promote significant alongshore and/or cross-shore transport.

Using flume experiments, Folkard (2005) investigated the hydrodynamic changes within *P. oceanica* patches in detail in a shallow water environment. His findings provided a better understanding of the nature of the turbulent waves produced by seagrass patches and how this can affect conditions within other patches. Folkard's study has been the basis for further experiments carried out in more recent years. Using large flume experiments, Stratigaki et al. (2011) and Manca et al. (2012) quantified the wave energy decay and

wave-induced flow effects of *P. oceanica* meadows in shallow water conditions. These experiments have confirmed that meadows are effective at reducing wave energy, especially for waves with low energy and small amplitude. Under these conditions, meadows are able to enhance sediment stabilisation relative to unvegetated patches of the seafloor. However, under high energy/large amplitude wave conditions, *P. oceanica* is less efficient at reducing wave energy, and thus does not offer significant beach protection against erosion during storms (Manca et al., 2012).

In this field, Infantes et al. (2012) used seafloor mounted Acoustic Doppler Velocimeters (ADVs) to evaluate wave attenuation induced by meadows directly, finding that *P. oceanica* meadows reduce wave height reaching the beach and raised the importance of the parameters k_s (equivalent bottom roughness) and C_D (drag coefficient) in wave propagation models over seagrass meadows. These observations are in good agreement with flume experiments and can be used to predict key hydrodynamic parameters, such as the wave friction factor (f_w) and the drag coefficient (C_D), in presence of meadows and, consequently, to quantify wave attenuation during storms.

Seedling tolerance for both *P. oceanica* and *Cymodocea nodosa* (Ucria) Ascherson (the second most common seagrass in the Mediterranean) has also been studied using a combination of flume experiments and field observation (Infantes et al., 2011). Finding that *C. nodosa* seedling are more tolerant to higher wave energies than *P. oceanica*. These studies have confirmed the assumption of Den Hartog (1972) that pioneer colonisation by *C. nodosa* may promote stabilization of the seafloor and facilitate the subsequent *P. oceanica* meadow development.

4.2. Influence of nearshore hydrodynamics on meadow development

Recognising the influence of seagrass meadows on nearshore hydrodynamics, recent research has also demonstrated a strong control of nearshore hydrodynamics on the morphology and bathymetrical distribution of seagrass meadows themselves (Infantes et al., 2009; Vacchi et al., 2010, 2012, 2014a). Infantes et al. (2009) provide a methodology to estimate the position of the landward, or upper, limit of *P. oceanica* meadows as a response to wave energy showing that an increase in wave energy is related to a decrease in *P. oceanica* cover, and that above a threshold wave energy, no seagrass is present. In Cala Millor (Mallorca Island, Spain), the threshold near-bottom orbital velocity above which the long-term persistence of

P. oceanica meadows (in a shallow bay) is compromised was ~40 cm·s^{-1} (Infantes et al., 2009). Wave breaking was also suggested to have a role in establishing the upper limit of meadows, although the position at which waves break changes seasonally, depending on wave parameters (height, period and length). Vacchi et al. (2010, 2014a) solved this problem in a study of 16 meadows in Liguria (NW Italy) by using annual wave climate data (i.e., height, period and length of waves with a 1 year return time derived from analysis of off-shore buoy records). Using this approach, the annual breaking depth (i.e., the still-water depth at the point where a wave breaks, calculated with offshore wave height with a return time of 1 year), represents the major constraint for the landward development of the meadows occurring on sedimentary beds; *P. oceanica* meadows do not occur shallower than these breaking depths (Vacchi et al., 2010, 2014a). Along the profile of a submerged beach, three distinct hydrodynamic zones can be recognised within the shallow portion of *P. oceanica* meadows (Figure 4B): (i) zone **a**, from the shoreline to the breaking depth (d_b), is unfavourable to the development of the meadow; (ii) in zone **b**, between the breaking depth and the closure depth (d_c), i.e., the depth where wave action on the seafloor becomes negligible (Sorensen, 2006), the meadow exhibits stunted development. In this zone, hydrodynamics majorly influence meadow architecture. Reduced cover of living *P. oceanica* and the occurrence of dead matte (resulting from a natural processes) characterise this zone; (iii) in zone **c**, beyond the closure depth, hydrodynamic conditions have little influence on meadow architecture, meaning that anthropogenic pressures are primarily responsible for any meadow degradation observed in this zone (Vacchi et al., 2010).

Predicting species and habitat distribution is extremely useful to support implementation of environmental legislation, protection and conservation measures, and ecosystem-based management in marine waters (Valle et al., 2011). In this respect, predictive models have been developed that are capable of identifying the region of the seafloor where the upper limit of meadows would lay under undisturbed conditions (i.e., those regions governed only by hydrodynamics, in absence of significant anthropogenic impact: Vacchi et al., 2014a). Such models have been validated at the local scale (Regione Liguria, NW Italy) and preliminary investigations at the regional scale (Western Mediterranean) have confirmed suitability for meadows developing on sedimentary substrates (Misson et al., 2014). In this context, the linear distance between a meadow's upper limit and the breaking depth shows a significant correlation with beach morphodynamics expressed by the surf scaling index ε (Jackson et al., 2005).

Based on this modelling, the two boundaries of the seafloor region within which the *P. oceanica* upper limit is expected to develop (under natural conditions) are given by (Figure 4B):

$$\text{i) } \kappa_{min} = 5.94 + 0.29\varepsilon$$

$$\text{ii) } \kappa_{max} = 17.83 + 0.41\varepsilon$$

where $\varepsilon = a\omega^2/g \cdot tan^2\beta$; a (breaker amplitude) = $H_0/2$ with H_0 = breaker height; ω (incident wave radian energy) = $2\pi/T_0$ and T_0 = period; g = acceleration of gravity; β = the slope of the beach in the surf zone.

At greater depths, light requirements for seagrass growth have been the major focus of research, and different quantitative models provide predictions for the lower growth limit. For *P. oceanica* meadows, this lower (or seaward) limit is traditionally considered under the sole influence of light penetration (Duarte, 1991):

$$\ln Zc = 0.26 - 1.07 \cdot \ln K,$$

where Zc is the depth of the meadow lower limit (in metres), and K is the coefficient of light attenuation underwater.

Duarte's equation is adequate for exposed areas, where hydrodynamics plays a relatively minor role compared to light penetration and water transparency, which are the primary controls on the position of meadow lower limits. However, hydrodynamics may have a significant influence on lower limits in sheltered bays or in coastal areas not exposed to intense storm waves (Vacchi et al., 2012). In these cases, the storm wave base (i.e., the limit of interaction between waves and seafloor, corresponding to $L_0/2$, where L_0 is the offshore wavelength: Svendsen, 2006) also plays an important role. Thus, in sheltered bays, the following equation should be flanked to Duarte's (1991) in order to predict the natural position of the lower limit of *P. oceanica* meadows:

$$Zc = 0.32 \cdot L_0 + 5.62,$$

where Zc is the depth of the meadow lower limit (in metres), and L_0 is the annual offshore wave length (in metres), computed as a climatologic mean (Figure 4A).

Together with hydrodynamic constrains and light availability, sediment size distribution has also been recognised as an important environmental control on seagrass development (Koch and Gust, 1999). Species distribution models (SDMs) accounting for these three factors are now being developed, offering significant

opportunities for informing management decisions based on local environmental conditions (e.g., Adams et al., 2015).

5. *Posidonia oceanica* and seafloor geomorphology

The interactions between organisms and abiotic seafloor features might play a significant role on benthic communities, affecting not only initial colonisation but also later assemblages and associated motile fauna though cascading effects (e.g., Guidetti et al., 2004; Kendrick et al., 2005). For example, the influence of substratum surface texture and physico-chemical properties on larval and spore settlement and recruitment, and benthic community composition and structure has been recognised (e.g. Cerrano et al., 1999; Bavestrello et al., 2000; Schiaparelli et al., 2003).

In contrast, no evidence of mineralogical control has yet been described for seagrass meadows developing on rocky substrata.

In the Ligurian Sea, *P. oceanica* meadows colonise both carbonatic (e.g., Bergeggi Island, Liguria, NW Italy) and quartzitic (e.g., Gallinara Island, Liguria, NW Italy) rocky substrata (Rovere et al., 2010b, 2015). In the MPA Tavolara-Capo Coda Cavallo (NE Sardinia), the geological switch between limestone and granite is not associated with significant changes in meadow spatial patterns (Rovere et al., 2013).

In Ventimiglia (Western Liguria, NW Italy) investigations of unusual patterns of *P. oceanica* in shallow water have been recently carried out (Montefalcone et al., 2014). In two areas, seafloor geomorphology was characterised by rocky outcrops alternating with sandy channels running orthogonal to the shoreline (Figure 5A). Here *P. oceanica* is only present on the harder and less erodible sandstone whilst being absent on the more altered and erodible marl, which remains covered by a layer of soft-sediments (Figure 5A).

These observations suggest that, in high-energy conditions, *P. oceanica* colonises preferentially the rocky seafloor instead of the sandy one. Thanks to root plasticity (Balestri et al., 2015), *P. oceanica* can anchor its rhizomes to tenacious rock, thus resisting the stress of waves that would otherwise tear away plants rooted in the shifting sand. In this respect, meadows may therefore develop at depths shallower than those predicted by the morphodynamic model of Vacchi et al. (2014a).

Similar patterns have been found at Spargi Island (La Maddalena Archipelago, NE Sardinia, Figure 5B) where the upper limit of meadow on the sandy seafloor is placed at ca. 4 m depth at around 80 m from the

shoreline compared to a depth of ca. 1 m and distance of around 15 m from the shoreline on adjacent sections of meadow on rocky substrata (Figure 5B). These observations, and others in different areas of La Maddalena Archipelago, indicate that the spatial distribution of *P. oceanica* is further constrained (to some extent) by substratum characteristics. Survival in exposed, high energy locations may only be possible where plants are able to colonise rocky substrates, on which attachments strength is presumably increased and the probably of loss by erosion reduced. More work is needed to clarify these potential interactions, necessarily incorporating observations on recruitment and mortality on rocky and sandy substrata under comparable wave conditions.

5. Future research directions

More than 20 years ago Fonseca and Cahalan (1992, abstract) stated that "Seagrasses are able to modify current flow and sediment composition, yet little information exists describing their effect on waves". Whilst progress has clearly been made on the interactions between *Posidonia oceanica* meadows and coastal geomorphology, sediment dynamics wave conditions and beach morphodynamics, many gaps remain in our understanding of *P. oceanica* biogeomorphology. There is good evidence that geomorphological and environmental features control the development not only of *P. oceanica* meadows but also of other marine and near-shore vegetation communities, including other seagrass species (e.g., Adams et al., 2015).

Future research effort should be given to the development or improvement of predictive models to define baseline reference conditions that will prove valuable in a management and conservation context (Vacchi et al., 2014b; Adams et al., 2015; Lyons et al., 2013). As with many other important biogenic habitats (e.g., tidal marshes, mangroves and coral reefs), seagrass meadows occur in close proximity to densely populated coastal regions, meaning that these habitats are facing increasing pressures due to human activity (e.g., Bostrom et al., 2011).

Multiple and cumulative human impacts lead to the degradation of healthy *P. oceanica* meadows implying structural and compositional loss, accompanied by a reduction of ecosystem functioning (Giakoumi et al., 2015; Montefalcone et al., 2015). Changes can be evaluated by comparing present ecosystem status to a predicted reference condition (e.g. Downie et al., 2013; Vacchi et al., 2014b). Further, an assessment of ecosystem services provided by *P. oceanica*, indicate an economic value for this habitat type of 172 € m^{-2} a^{-1}

(Vassallo et al., 2013). Defining reference conditions against which the economic impact of meadow losses can be estimated offers a valuable approach to raising awareness of conservation needs under a framework of ecosystem services.

For such approaches to be effective, we suggest that a wide range of littoral physical parameters need to be carefully considered in modelling. For example, there is now evidence that degraded upper limits of *P. oceanica* meadows may be induced by hydrodynamic conditions rather than solely due to anthropogenic factors, as has often been assumed (Bianchi and Peirano, 1995; Boudouresque et al., 2012). Future investigations of other widely-distributed Mediterranean seagrasses, such as *C. nodosa*, *Zostera* (*Zostera*) *marina* Linnaeus and *Zostera* (*Zosterella*) *noltei*, should also consider a biogeomorphological approach to assessing the development, functionality and possible regression of these meadows. Indeed, even if meadows composed of these other species are presumed to play a less important role than *P. oceanica* (e.g., Pergent et al., 2013), their interactions within the Mediterranean littoral system have seldom been explored quantitatively (Infantes et al., 2011; Paquier et al., 2014).

Predicting the medium-term evolution of *P. oceanica* meadows in the Anthropocene is particularly challenging, especially under scenarios of climate change (Bianchi et al., 2012). The effects of climate change on marine ecosystems are both physical and chemical, including augmentation of sea water temperature, sea level rise, modification of wave frequency and height, and ocean acidification (Planton et al., 2012 and references therein). All these effects are expected to influence *P. oceanica* meadows in various ways, but predictions are difficult because synergisms, interactions and feedbacks will complicate their impacts compared to direct influences alone. For example, the phenology of flowering of *P. oceanica* would be facilitated in a warmer Mediterranean Sea (Diaz-Almela et al., 2007; but see Montefalcone et al., 2013 for a critical view), yet vegetative growth may be hampered (Marbà and Duarte, 2010; Jordà et al., 2012). Plant vitality has also declined in coincidence with recent positive, climatic anomalies (Pergent et al., 2014). Sea level rise may be supposed to cause the upward displacement of both lower and upper limits of *P. oceanica* meadows. However, withdrawal of the lower limit has been recently documented off Corsica (Pergent et al., 2015), and may be amplified by increasing turbidity due to changing rainfall regimes and human pressures (Gatti et al., 2015), which are both expected to intensify. On the other hand, the potential landward shift of

the upper limit of meadows will be limited by the intense human impacts in the Mediterranean region (Peirano and Bianchi, 1997; Montefalcone et al., 2010).

This general picture is further complicated by an expected decrease in mean significant wave height (Planton et al., 2012), altering both the breaking depth and offshore wave length. Assuming that morphodynamic models (e.g., Vacchi et al., 2014a) will hold under the new wave regimes, these should prove helpful for predicting the future positions of meadows. Rising sea level also has implications for enhanced coastal erosion and reduction in beach extent, which may in turn modify seagrass berm formation and cycling. Finally, ocean acidification will again complicate the expected patterns with antagonistic outcomes. A first example concerns calcified epiphytes, which are supposed to protect *P. oceanica* leaves against grazing: their decline under lower pH conditions might therefore allow for a greater impact of herbivory on seagrass ecosystem functioning. As a second example, the higher concentration of CO_2 might enhance photosynthesis at the compensation depth, thus counterbalancing the negative effects of light reduction by increased turbidity. Additive models that build on those we have described, incorporating updated information presented by IPCC (Intergovernmental Panel on Climate Change) Fifth assessment report (AR5) are needed to disentangle these complexities, to provide usable predictions for management decisions.

Over much longer periods of time (i.e., millennial scale), an understudied aspect of meadow biogeomorphology is coastal landscape evolution. Other than the pioneering investigation by Mateo et al. (2001) on the utilisation of *P. oceanica* as a proxy for tracking paleo-coastal environmental changes, studies exploring the interactions between Mediterranean seagrasses and coastal evolution during the Holocene are rare (e.g., Rovere et al., 2010a; Serrano et al., 2011). Recent long-term analyses on the evolution of Shark Bay (Australia) have revealed a key role of seagrass meadows (mainly *Amphibolis* spp) since the early Holocene (12-8 ka BP, Bufarale and Collins, 2015) in controlling the production and deposition of a significant amount of bioclastic sediments (Bufarale and Collins, 2015). Comparable investigations are presently lacking for *P. oceanica* despite its occurrence in sedimentary records from paleogeographic reconstructions along the Mediterranean coasts (e.g., Morhange et al., 2000; Rovere et al., 2010a).

The ecological and geomorphological role of *P. oceanica* meadows in Mediterranean coastal environments has been compared to that of coral reefs in tropical seas (Boudouresque and Meinesz, 1982). Thanks to the accretion of matte structures, *P. oceanica* can, similarly to coral reefs, impart a positive topography to the

seafloor, sometimes reaching the sea surface under suitable conditions. No other seagrass species has a comparable bioconstructional capacity. That seagrass matte represents a true bioconstruction is perhaps debatable, as it is not a mineralised (carbonatic) structure and the contribution to $CaCO_3$ deposition is only indirect (Bianchi, 2001). The matte may persist with little morphological alteration for millennia (Mateo et al., 1997), but its deposits develop at a rate of 0.06 to 0.41 $cm \cdot a^{-1}$, which is an order of magnitude lower than coral reefs aggradation rates (Sorokin, 1993; Pichon, 1995). Coral reefs are considered the ideal locale for marine studies at the interface between ecology and geology (Bianchi et al., 1997), and a similar attitude might be usefully applied to seagrass species worldwide, and especially to *P. oceanica* in the Mediterranean Sea.

We believe that a biogeomorphological approach, integrating biology, ecology, sedimentology and geomorphology through a collaborative effort of specialists belonging to different disciplines, will continue to offer new insights to the study of seagrass meadows. Ultimately, the ongoing development of models able to describe and predict biogeomorphological processes and dynamics of seagrass meadows, particularly under future scenarios of climate change, will prove essential for conservation and management efforts of these important ecosystems.

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Table 1. Typology of the lower (seaward) limits of *Posidonia oceanica* meadows.

SHADED LIMIT	
Limiting factor to seagrass development: light availability	
Seagrass substratum cover < 50%	
NATURAL CONDITION	REGRESSED CONDITION
Plagiotropic rhizomes, no matte	Dead plagiotropic rhizomes, remnant shoots on dead matte
1) Limit progressive (tracing rhizomes)	
a) with long rhizomes (rows perpendicular to depth contours)	
b) with short rhizomes (often branching)	
2) Limit irregular (patchy)	
SHARP LIMIT	
Limiting factor to seagrass development: substratum nature	
Seagrass substratum cover > 50%	
NATURAL CONDITION	REGRESSED CONDITION
Orthotropic rhizomes, matte low	Undermined orthotropic rhizomes
ERODED LIMIT	
Limiting factor to seagrass development: bottom currents	
Seagrass substratum cover > 75%	
NATURAL CONDITION	REGRESSED CONDITION
Matte > 20 cm high, exposed, with cliff	Sparse shoots on dead eroded matte
1) linear (alongshore currents)	
2) digitate, sometimes with patches (ripple currents)	

Figure captions:

Figure 1. Distribution of *Posidonia oceanica* (red line) along the coast of the Mediterranean Sea (modified after Giakoumi et al., 2012).

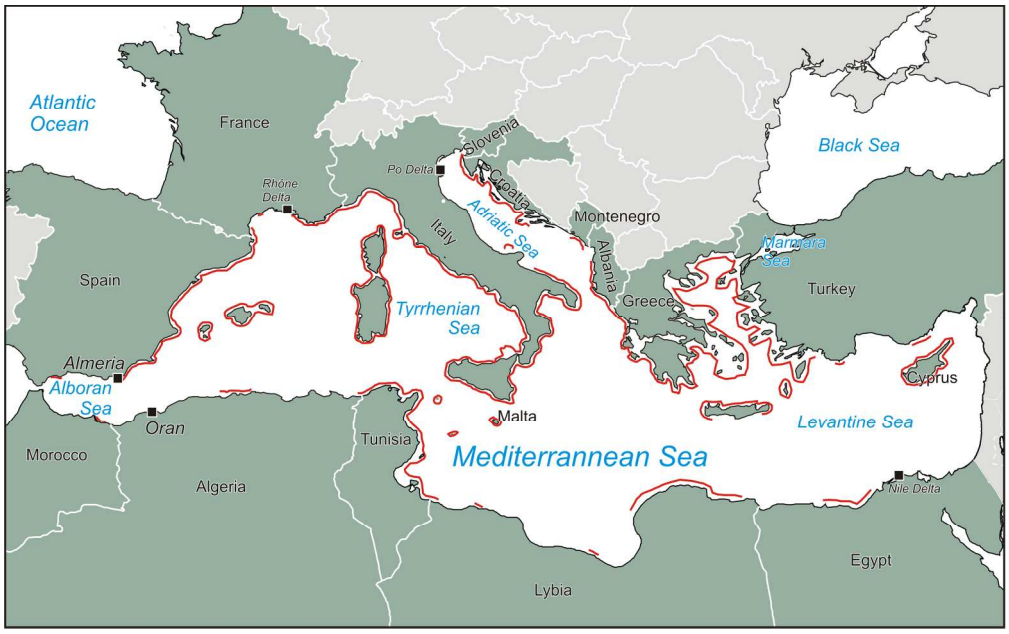
Figure 2. Scheme of the putative effects of sea water acidification on the carbonate production of *Posidonia oceanica* meadows and other Mediterranean carbonate factories (modified after Bianchi et al., 2012). The different size of compartment symbols indicates change in relative importance under ocean acidification.

Figure 3. Relationship between *Posidonia oceanica* leaf litter, sediment exchanges and beach morphology in (a) sheltered and (b) wave exposed environments.

Figure 4. Hydrodynamic constraints on lower (deeper, panel A) and upper (shallower, panel B) limits of the *Posidonia oceanica* meadows (modified after Vacchi et al., 2010, 2012 and 2014a). In panel A, L_0 is the off shore wave height (1 year return time) and Z_c is the meadow lower limit depth. In panel B, κ_{min} et κ_{max} define the two boundaries of a seafloor region where the predicted upper limit of *P. oceanica* would be located under natural conditions; d_b, and d_c are the breaking depth and closure depth, respectively (1 year return time); a, b and c represent the three dynamic zones of the upper portion of the meadow (modified after Vacchi et al., 2010).

Figure 5. *Posidonia oceanica* selective colonisation and/or survival at shallow depths. A) Ventimiglia, Western Liguria, NW Mediterranean. The meadow is only present on the rocky seafloor, whereas the sandy seafloor remains unvegetated (modified after Montefalcone et al., 2014). The presence of the fold is speculative and based on terrestrial measures of strata strike and dip. Sd is sandstone, Ma is marl. B) Spargi Island, Northern Sardinia, W Mediterranean. The upper limit of the meadow occurring on a sandy substrate (I) is placed at around ~-3 m depth and at

around ~80 m from the shoreline. The upper limit on rocky substrata (II) is shallower (around -1 and ~15 m from the shoreline) in the portion of the meadow occurring on rocky substrate (II).



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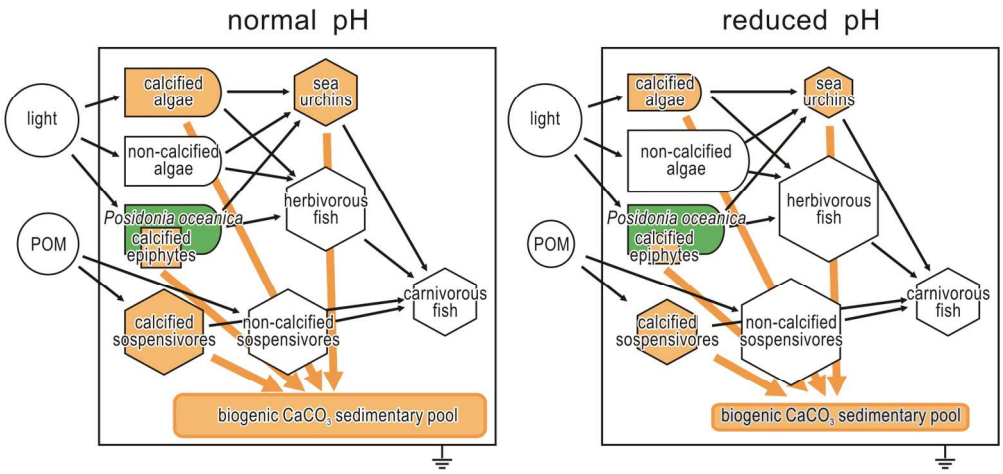

Figure 2. Scheme of the putative effects of sea water acidification on the carbonate production of Posidonia oceanica meadows and other Mediterranean carbonate factories (modified after Bianchi et al., 2012). The different size of compartment symbols indicates change in relative importance under ocean acidification.
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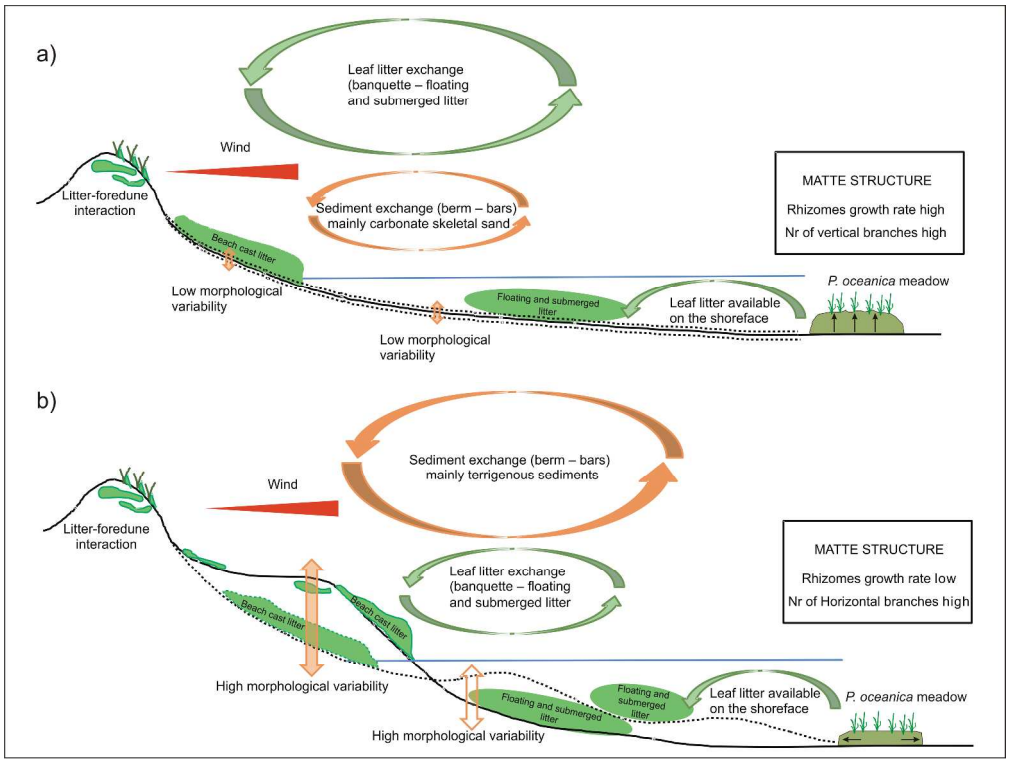

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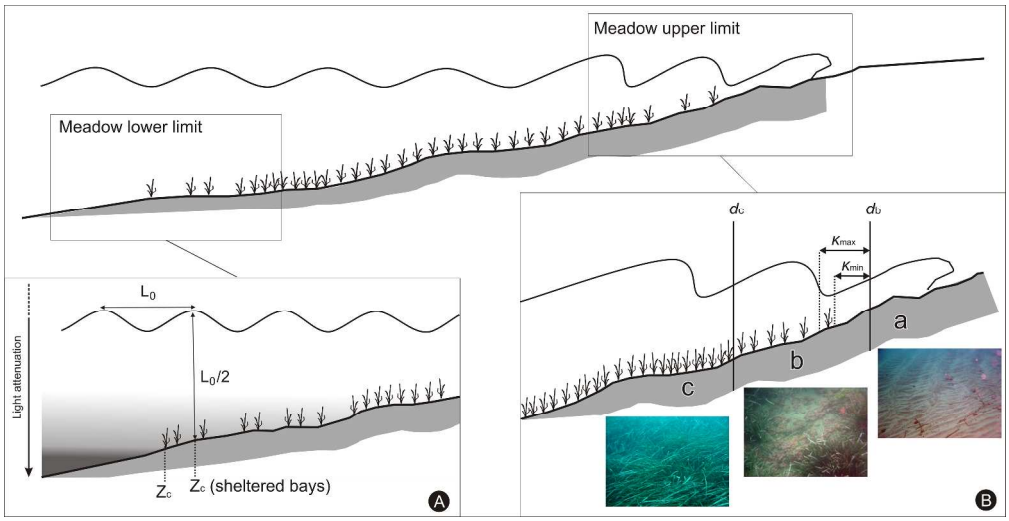
372x280mm (300 x 300 DPI)



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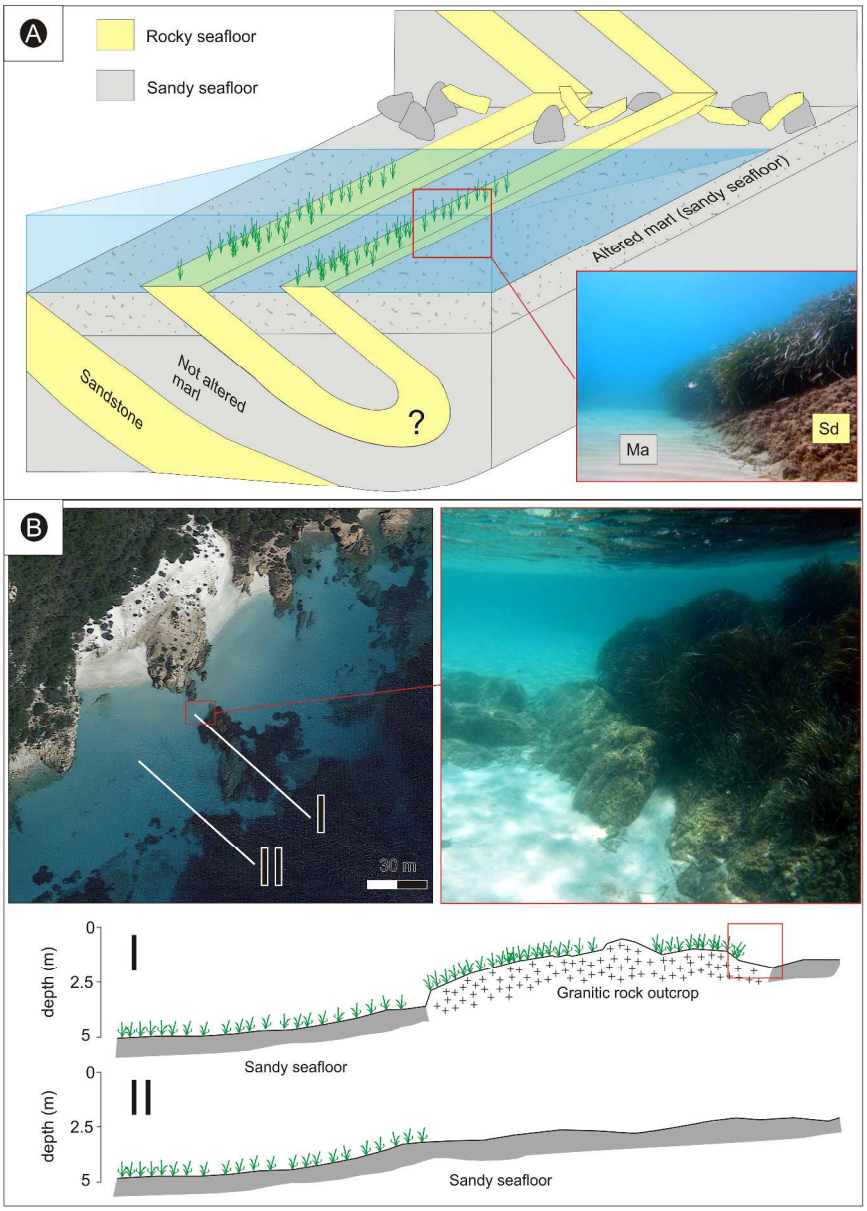

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447x610mm (300 x 300 DPI)