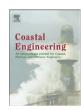
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The role of seagrasses in coastal protection in a changing climate



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ABSTRACT

The contribution of seagrasses to coastal protection is examined through the review of the most relevant existing knowledge. Seagrasses are the largest submerged aquatic vegetation ecosystem protected in Europe and it is worth examining their contribution to coastal protection. The review performed highlights incident energy flux, density, standing biomass and plant stiffness as the main physical and biological factors influencing the efficiency of the protection provided by seagrasses. The main conclusion achieved is that seagrass meadows cannot protect shorelines in every location and/or scenario. The optimal conditions for enhancing the protection supplied might be achieved in shallow waters and low wave energy environments, with high interaction surface, at the vertical and horizontal dimension, between water flow and seagrasses. Likewise, the most favorable protection might be provided by large, long living and slow growing seagrass species, with biomass being largely independent of seasonal fluctuations and with the maximum standing biomass reached under the highest hydrodynamic forcings. It is shown that seawater warming, increasing storms and sea level rise, together with the increasing population and anthropogenic threats in the coastal area may lead to rates of change too fast to allow seagrasses to adapt and keep their coastal defense service. Finally, to amend the decline of seagrasses and consequent coastal protection loss, different artificial and natural adaptation measures are provided.

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1. Introduction

Coastal ecosystems are some of the most heavily used and threatened natural systems (Halpern et al., 2008; Lotze et al., 2006). The consequence, is an overall decline which is affecting a number of critical benefits (Barbier et al., 2011). In the European Union the coastline extends over approximately 170,000 km and host more than 70 million inhabitants. A great length of this highly populated and economical important coastline is seriously threatened by erosion and flooding (Alcamo et al., 2007). Existing literature and IPCC scenarios point to an increase in sea level rise (Nicholls et al., 2007) and in the frequency and intensity of extreme events associated with waves (Izaguirre et al., 2011) and sea levels (Menendez and Woodworth, 2010), resulting in a significant increase in the number and severity of flood events and erosion.

Traditionally, the protection of coastal areas from flooding is approached from an engineering perspective (e.g. seawalls and bulkheads; Borsje et al., 2011). However, the increasing rate of global climate change experienced in the last decades and projected for the coming ones, emphasizes the need for innovative approaches to protect

the (European) coasts. In recent years the number of initiatives proposing soft mitigation actions to reduce the risk of flooding and erosion has been considerably augmented. Coastal protection systems can benefit from ecosystem engineers, organisms that modify the local physical environment causing changes in biotic or abiotic materials by their structures or activities (Jones et al., 1994). Although ecological options may not always provide the required defense, combining engineering and ecology seems a promising way toward innovative coastal protection solutions (Bouma et al., 2014-this volume). The literature provides sufficient evidences about the capacity of submerged aquatic vegetation to physically and chemically engineer their environment and to supply coastal protection services, a term applied to describe the benefits human populations obtain from the ecosystem functions (Millennium Ecosystem Assessment, 2005). Seagrasses are one of such ecosystems. Besides being the largest submerged aquatic vegetation ecosystem protected in Europe (included in the Directive 92/43/EEC), they play an important ecological role providing highly valuable ecosystem services, including coastal protection. These singularities justify the interest in analyzing its potential contribution to coastal adaptation to climate change. The interaction of seagrass beds with hydrodynamics is widely recognized to affect wave attenuation (Fonseca and Callahan, 1992; Koch et al., 2006; Paul et al., 2012; Ward et al., 1984), current flow (Fonseca and Fisher, 1986; Fonseca et al., 1982; Peterson et al., 2004; Sand-Jensen and Mebus, 1996), and sediment dynamics (Chen et al., 2007; De Boer, 2007; Fonseca, 1989; Madsen et al., 2001; Scoffin, 1970; Wanless, 1981).

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The possibility of taking advantage of the coastal protection offered by natural habitats as part of potential adaptation options is examined here. Assessing the feasibility of using seagrass meadows for coastal defense within Europe is not an easy task to solve, as management solutions must consider which species and traits drive coastal protection by seagrasses, but also what ecosystem dynamics may affect the predictability of services provided by seagrass beds (Paul et al., 2012). To find answers to these questions we review existing knowledge with the purpose of understanding: (1) What are the mechanisms governing the coastal protection provided by seagrasses; (2) what are the main experimental and numerical advances in the studies of wave attenuation; (3) how natural and anthropogenic threats can deteriorate the protection provided; and (4) what adaptation measures could be implemented.

2. Ecological functions of seagrasses

Seagrasses are the unique group of flowering plants adapted to exist fully submerged. The large areas occupied in the Mediterranean (25% of the sea bottom between 0–40 m depths) and the Atlantic (Fig. 1) and the valuable coastal services provided (Costanza et al., 1997; Orth et al., 2006), make seagrasses a good candidate for climate change

adaptation. Of about 60 species worldwide, seven seagrass species are found on Europe (Halophila decipiens, Cymodocea nodosa, Posidonia oceanica, Zostera marina, Zostera noltii, Ruppia maritima and Halophila stipulacea) and four are native to the European temperate waters (Fig. 1): Zostera marina, Zostera noltii, Posidonia oceanica and Cymodocea nodosa. Z. marina are found in coastal and estuarine areas, from the intertidal to the subtidal, and from sheltered to exposed coasts (Table 1). It occurs predominantly in mono-culture throughout most of its distribution, although in the eastern North Atlantic and Mediterranean it might coexist with Z. noltii (Larkum et al., 2006). Z. noltii is distributed in the Mediterranean and along the Atlantic coasts of Europe and northern Africa growing from intertidal flats to subtidal depths of 1–2 m. P. oceanica is a Mediterranean endemic seagrass and the climax community of a successional process which forms large underwater monospecific meadows at depths from 1-60 meters depending on water clarity. C. nodosa is a warm water species found mostly in the subtidal and widely distributed in the Mediterranean, Canary Islands and down the North African coast.

From an ecological point of view, seagrasses are habitat-forming ecosystem engineers that facilitate many other species (Hoegh-Guldberg and Bruno, 2010) and play a relevant role in ecological processes, including trophic transfers to adjacent habitats (Costanza et al., 1997) such as saltmarshes, biogenic reefs (e.g. mussel and oyster

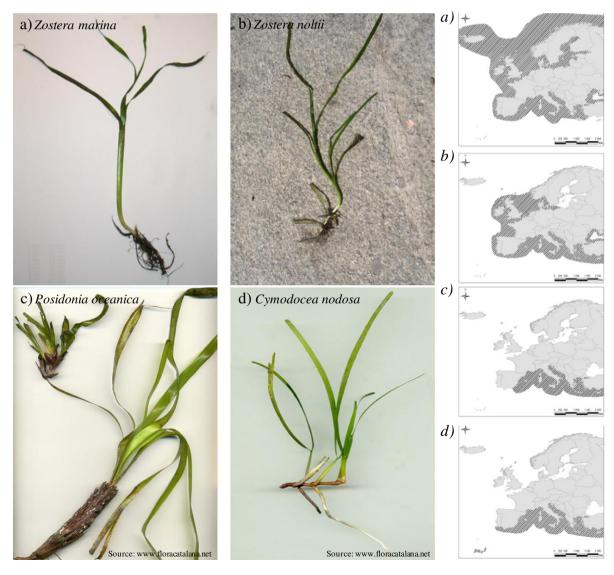


Fig. 1. Detail of the morphology and geographical distribution of Zostera marina, Zostera noltii, Posidonia oceanica and Cymodocea nodosa in the European coastal waters (From Borum et al., 2004).

Table 1Geographical distribution, habitat, tidal conditions, morphological and architectural features and growth rates of native European seagrass species. Average range values are indicated. nd: no data. (Revised from Borum et al. (2004); Larkum et al. (2006); Short et al. (2007)).

	Zostera marina	Zostera noltii	Posidonia oceanica	Cymodocea nodosa
Geographical distribution in Europe	Atlantic (except Canary islands) from the Arctic waters (Iceland) to the southern coast of Spain. Mediterranean and Black sea	Atlantic from the southern coasts of Norway to the Canary Islands, Mediterranean and Black sea	Mediterranean	Atlantic (just in the Canary islands) and Mediterranean
Habitat	Estuaries, coastal waters and lagoons	Estuaries, coastal waters and lagoons	Coastal waters and lagoons	Coastal waters, lagoons
Tidal conditions	Subtidal	Intertidal and shallow subtidal waters	Subtidal	Subtidal
Maximum depth (m)	15	10	50-60	50-60
Nº leaves	3–7	2–5	5–10	2-5
Leaf width (mm)	2-10	0.5-2	5–12	2-4
Leaf length (cm)	30-150	5-25	20-40	10-45
Above-ground biomass (mg DW ⁻¹)	272.5	6.5	731.0	82.8
Shoot elongation rate (cm day ⁻¹)	3.2	0.7	0.8	1.3
Shoot life span (days)	554.8	nd	4373	876
Rhizomes thickness (mm)	2–6	0.5–2	5–10	3

reefs) and soft-bottom invertebrate fauna (Eaton et al., 1995). Seagrass habitats have relatively high primary productivity (Waycott et al., 2009), and by providing shelter from predation, can support high biodiversity and faunal density and biomass (Hemminga and Duarte, 2000). Moreover, they provide important nursery grounds and feeding areas (Short and Neckles, 1999; Unsworth et al., 2008; Watson et al., 1993). Seagrass beds also improve water transparency and quality through trapping and storing solids particles and dissolved nutrients (Short et al., 2007). They also supply an important source of carbon to the detrital pool, some of which is exported to the deep sea (Suchanek et al., 1985), although much of the excess organic carbon produced is buried within seagrass sediments, which are hotspots for carbon sequestration (Duarte et al., 2005).

From a physical point of view, seagrasses are able to significantly influence the hydrodynamic environment by reducing current velocity, dissipating wave energy and stabilizing the sediment. They modify the habitat they colonize (Koch, 2001; Moriarty and Boon, 1989) through the increase in sediment deposition and silt content. As a result, seagrasses reduce turbidity and increase light availability, which in turn promote their growth and reproduction (Van der Heide et al., 2007).

Summarizing, seagrass can be related to a wide range of valuable ecosystem services, including a number of services related with the mitigation of climate change effects such as the coastal protection, erosion control and carbon sequestration (Barbier et al., 2011; Orth et al., 2006). Among all of them, coastal protection has gained strong interest over the last decade because of the need for measures that minimize anthropogenic impacts of coastal protection structures on coastal ecosystems (Borsje et al., 2011).

3. Mechanism of the coastal protection provided by seagrasses

3.1. Physical processes governing the coastal protection

Coastal defense provided by seagrasses depends on its capacity to attenuate the processes of flooding and coastal erosion, which have been identified as the main natural threats for coasts (Borsje et al., 2011; Duarte et al. (2013); Granek et al., 2009) (Fig. 2). A range of dynamics are central to both processes (e.g. mean sea level, tide, storm surges, waves and currents) and will most probably be affected by climate change.

There are three mechanisms that contribute directly to the protection of the coast by decreasing the intensity of incoming energy: (1) energy dissipation due to wave breaking; (2) energy dissipation due to friction; (3) energy reflection in the offshore direction (Duarte et al., 2013; Koch et al., 2006). These mechanisms can be triggered by seagrasses as well as by other natural or artificial obstacles. Seagrasses produce negligible energy reflection and low wave attenuation by friction, while most of the artificial structures (not only offshore but also

at the shoreline) give rise to higher energy reflection and wave attenuation by breaking and friction. Artificial solutions also lead to stronger changes in nearshore currents, which in turn can cause more severe modifications at the coastline. Seagrass ecosystems provide a complementary benefit; they are capable to protect the coast through an indirect mechanism related with their capacity to stabilize and maintain sediments in shallow areas. Furthermore, in contrast to artificial structures, natural adaptation to climate change is possible for seagrasses which in turns means that they are able to naturally maintain their coastal protection services (Borsje et al., 2011). For example, increased dissolved CO₂ concentrations promote seagrass growth (Palacios and Zimmerman, 2007), increases in water velocity may contribute to plant productivity in some locations (Fonseca and Kenworthy, 1987), increases in sediment load may promote the sedimentation and accretion rate and genetic diversity could help the plants to cope with higher temperatures (Ehlers et al., 2008). All of these and other mechanisms make seagrasses capable to adapt to climate change if the changes occur at slow enough rate to allow such adaptation.

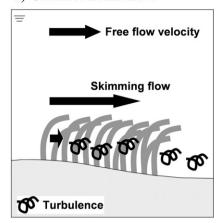
Submerged seagrasses interact with and modify both current flows and wave action. In the case of unidirectional flow (Fig. 2a), seagrass meadows reduce current velocities within the canopy through deflection of the water flow over the canopy and loss of momentum within the canopy by the frictional effects of vegetation (Fonseca et al., 1982; Koch et al., 2006; Peterson et al., 2004). An accelerated current over the canopy (skimming flow) is frequently developed as consequence of the strong discontinuity in the drag force between the area occupied by the meadow and the free flow over it (Fonseca et al., 1982; Gambi et al., 1990; Thompson et al., 2004). Inside the meadow the main mechanism for momentum exchange is the longitudinal advection (Nepf and Vivoni, 2000) and the turbulence source of the leave wakes.

In the oscillatory flow (Fig. 2b) the orbital motion produces a periodic movement of the leaves, with the amplitude being strongly dependent on the stiffness of the plants (Bouma et al., 2005, 2010). Orbital velocities at the top of the canopy are modified due to drag discontinuity, which propagates in the wave direction as experimentally confirmed Stratigaki et al. (2011) and numerical Maza et al. (2013) for submerged posidonia meadows. The vertical motion associated to oscillatory conditions enhances the vertical penetration of the orbital velocities within the canopy, providing an important mixing layer on the top of it. Leave flexibility will influence the height of this mixing layer where water removal and nutrients transport is produced. As in the case of unidirectional flow, leave wakes are developed inside the meadow generating a reduction of the flow velocity.

Sediment stabilization by seagrasses makes up an indirect mechanism for coastal protection (Christianen et al., 2013). Both reduction in currents and wave attenuation by seagrasses not only increase sedimentation rates within meadows, but also decrease the potential for resuspension (Bouma et al., 2005; Hemminga and Duarte, 2000;

b) Waves

a) Unidirectional flow



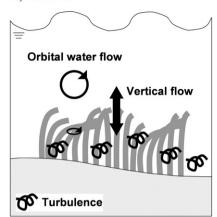


Fig. 2. Physical processes occurring in the interaction between flexible seagrasses and (a) unidirectional flow (currents) and (b) waves.

Madsen et al., 2001). Besides, the rhizoidal system of seagrasses contributes to the sediment stabilization and the control of the coastal erosion (Barbier et al., 2011).

3.2. Factors influencing the efficiency of the coastal protection

The efficiency of seagrasses reducing currents and waves and stabilizing the sediment is related to the water dynamic properties and the ecosystem and biological features of plants (Orth et al., 2006) (Table 2). The main dynamic properties affecting the capacity of seagrasses to attenuate flooding and erosion are wave period and incident energy flux, although the combination of different dynamics (unidirectional and orbital flow and water level) may also play an important role in the capacity of water to penetrate into the canopy (Koch et al., 2006). Meadows with highest wave attenuation and sediment stabilization capacities may be found at moderately energetic environments and under conditions of low period waves (Bradley and Houser, 2009). Therefore, differences in the coastal protection efficiency are expected as a result of seagrasses coastal distribution preferences and consequently on the hydrodynamic conditions each species is exposed (Table 1). While P. oceanica only grows in coastal areas, C. nodosa, Z. marina and Z. noltii are also found in estuaries and lagoons where wave action is reduced or even not present. Hence, sheltered areas and low period waves may represent the optimal conditions for enhancing the coastal protection provided by seagrasses (Bradley and Houser, 2009).

Regarding the ecosystem features, factors such as the relative water depth (water depth/canopy height), the relationship between the meadow width and the wavelength of incident dynamics or the sediment composition are also essential elements regulating the

effectiveness of coastal protection (Duarte et al., 2013). Seagrasses are more successful reducing waves and currents in shallow areas, when they occupy a higher proportion of the water column (Fonseca and Callahan, 1992; Koch et al., 2006; Ward et al., 1984). Precisely in shallow areas, the eelgrass *Z. noltii* and *Z. marina* can also reach high abundances while occupying a high proportion of the water column (Table 1), combining at the same time two important conditions in the coastal defense. Thus, a higher interaction surface, at the vertical and horizontal dimension, between water flow and seagrasses allows increasing the total hydrodynamic energy attenuation.

Stiffness, biomass, density, leaf length and morphology are major biological plant properties influencing the coastal protection value of seagrasses. The stiffness of leaves determines the drag forces exerted over the plants and the flow penetration in the meadow by leaves bending. The attenuation of wave and currents also depends on the aboveground biomass which is highly related with the number of shoots per unit area and number and size of leaves. P. oceanica is the European species with the longest and widest leaves, the highest number of leaves per shoot and in addition the highest above-ground biomass (Table 1). Accordingly, P. oceanica may be one of the species with highest capacity to attenuate hydrodynamic energy. In contrast, Z. noltii is the species with the lowest number of leaves, width and length, although it can reach very high values of density (22,000 shoots/m²) in the Mediterranean (Curiel et al, 1996). Another important factor is the morphology of the plants which may explain not only the vertical biomass distribution, but the current velocity profile within the meadow (Ackerman and Okubo, 1993; Gambi et al., 1990; Koch et al., 2006; van Keulen and Borowitzka, 2002). Some species, like Z. marina, show an accelerated flow at the bottom of the canopy due to biomass decreases near the

Quantification of the relative influence of water dynamics properties, ecosystem and biological features in the reduction of the current velocities, wave attenuation and sediment stabilization, as the main coastal protection aspects affected by seagrasses: very high influence; very high influence.

Factors influencing coastal protection		Current reduction	Wave attenuation	Sediment stabilization
Water dynamics properties	Wave period			<u> </u>
	Energy flux			
	Combination of dynamics	/		
Ecosystem features	Relative water depth			
	Relative meadow width			
	Sediment composition			
Biological features	Stiffness			
	Density/Above-ground biomass			✓
	Below-ground biomass			
	Leaf length			
	Morphology			

bottom. This effect is more marked when the plants bend and accumulate more biomass in the upper part of the canopy.

Sediment stabilization is influenced by the sediment trapping (Gacia et al., 2003) and flow velocity reduction provided by the above-ground biomass (Fonseca and Callahan, 1992; Gambi et al., 1990; Widdows et al, 2008), but also by the rhizoidal and root system (Hemminga and Duarte, 2000). For that reason, even the species with the lowest above-ground biomass (e.g. *Z. noltii*) must be considered for coastal protection, since it enhances the sediment stabilization and thereby the creation of shallows (Fonseca, 1989; Wilkie et al., 2012).

3.3. Fluctuations of the factors influencing the coastal protection

Within the aforementioned physical and biological factors, the effectiveness of coastal protection provided by seagrasses is subject to noticeable variations at the temporal scale. Seagrass habitats are stochastic environments where functions, processes and dynamics are governed by the physical, biological and chemical properties of the environment they live in. In temperate regions such as the European coasts main environmental factors regulating seagrasses dynamics, such as light and water temperature, are subject to well-defined seasonal patterns (maximal during summer and minimal during winter) which variations may trigger direct changes in the ecosystem structure (e.g. biomass, shoot density, etc) and indirect changes in the ecological functions and protection services (e.g. decreasing light levels may cause seagrass degradation or prolong the leaves of plants and thin the density of shoots).

Seagrasses are mostly perennial organisms that may reflect the seasonal environmental conditions (Borum et al., 2004), although the magnitude of the changes varies among species (Krause-Jensen et al., 2004). Large, long living and slow growing species such as *P. oceanica*, which may live for centuries, are more independent from seasonal changes than smaller and faster growing species with a short lifespan (e.g. *Z. noltii*). These fluctuations are important since seasonal changes might have direct effects on the wave attenuation capacity. Wave attenuation typically increases with standing biomass, shoot density and leaf length (Bouma et al., 2010; Paul et al., 2012). Thereby, wave attenuation is far from constant in time and might also fluctuate spatially, seasonally and interannually (Duarte et al., 2004).

Except for P. oceanica that grows more independently of seasonal variations in environmental factors (Krause-Jensen et al., 2004), biomass, shoot density and leaf length of European seagrasses is maximum during summer and minimal in the winter when growth almost ceases (Duarte and Chiscano, 1999; Koch et al., 2009; Marbà et al., 2004). The observed values at Santander (Spanish Atlantic coast) for Z. marina and Z. noltii confirm seasonal fluctuations in the above-ground biomass, shoot density and leaf length (Fig. 3). The detected pattern shows a noticeable peak for both species in summer (July-October), coincidence with the maximum values of water temperature, and a decrease in autumn and winter (October-January). The seasonal patterns result in the absence of high biomass meadows in those periods with the strongest winds, highest waves and highest storm surges (October to March; Fig. 3). Thus, the seasonality of seagrass growth imposes seasonal changes in the wave attenuation capacities and sediment trapping, with lowest effects when hydrodynamic forcing are the strongest. Moreover, the relationship of the above-ground biomass with the water temperature highlights the incidence the global warming effect might have on the coastal protection provided by seagrasses.

4. Methods to quantify the coastal protection provided by seagrasses

The interest in understanding how seagrass vegetation interacts with the hydrodynamics and contributes to coastal protection has lead to a growing number of experimental, field and numerical studies. Studies have been carried out from an ecological perspective, trying to enhance the knowledge about how the different species function within

the ecosystem, and from a more applied engineering perspective, trying to quantify how this vegetation can protect the coast by means of wave attenuation factors. In this section a detailed assessment of the literature is carried out, focusing on wave attenuation analysis as a first approximation to determine coastal protection. Although, other important features such as the effect of currents or sediment transport are important in coastal protection with seagrasses, they are not considered here in detail.

4.1. Experimental studies for measuring the coastal protection

Both field and laboratory observation of wave attenuation by submerged vegetation has been developed mainly due to the complexity of the physical processes involved in the interaction of waves with submerged vegetation. First, wave action on plants is driven for highly non-linear processes including turbulent flow within and around the vegetation meadow as a sink of momentum. Hydrodynamic param such as wave characteristics (height and period), water depth or plant submergence ratio (i.e.: Maza et al., 2013; Mendez and Losada, 2004; Stratigaki et al., 2011), have been shown to be relevant in wave damping assessment. Second, plant ecological and morphological factors such as shoot density, leaf length, plant stiffness or standing biomass (Bouma et al., 2005) has been proven to play and important and active role in wave attenuation. None of the existing physical approaches, laboratory and field, ensure a perfect assessment of wave attenuation, however, important features can be extracted from both approaches for a better understanding of the physical processes.

In the field, the main drawback is that both vegetation characteristics and hydrodynamic conditions cannot be properly controlled. Factors such as the seasonality of seagrass growth or random variation of standing biomass modify attenuation due to the heterogeneity of the meadows. In addition, technical problems associated to the record of valuable variables, such as flow velocities within the meadows without perturbing the flow patterns, are also present. As a result, the conclusions from the few available field studies on wave attenuation have not lead to generalizations yielding site specific results. However, besides the aforementioned limitations, field studies have the advantage of providing measurements under realistic and relevant physical conditions.

Field studies have been focused not only on direct measurements of wave attenuation but also on flow reduction, as a relevant parameter to characterize the effect of energy damping. Lacy and Hoover (2011) quantified the interaction of currents with *Z. marina* by measuring velocity over and inside the vegetation meadow. They concluded that eelgrass canopies generate significantly more roughness and drag than unvegetated areas, highlighting the importance of vegetation density in the magnitude of the effects. This aspect was also highlighted by Paul and Amos (2011) who noted the strong seasonality of *Z. noltii* and its implications in wave attenuation. They concluded that a minimum shoot density is required in order to observe wave attenuation. Therefore, the minimum density needed to produce hydrodynamic attenuation of each seagrass species is an important aspect that must be determined when dealing with coastal protection problems and it is not quantitatively declared yet.

Several studies have been also developed to determine wave attenuation produced by the *P. oceanica*. Infantes et al. (2011) validated seedling survival flume results with the field data obtained at four locations in the Mediterranean. In addition, Infantes et al. (2012) also measured wave heights and orbital velocities along a meadow finding attenuations around 50% for low wave height conditions. Similar values of attenuation were obtained by Tigny et al. (2007) who studied the effect of *P. oceanica* on the shoreline evolution. They concluded that these meadows significantly affect the littoral geomorphology, providing biogenic sediments, controlling beach slope, and attenuating hydrodynamic energy. However, the number of studies performed on other species

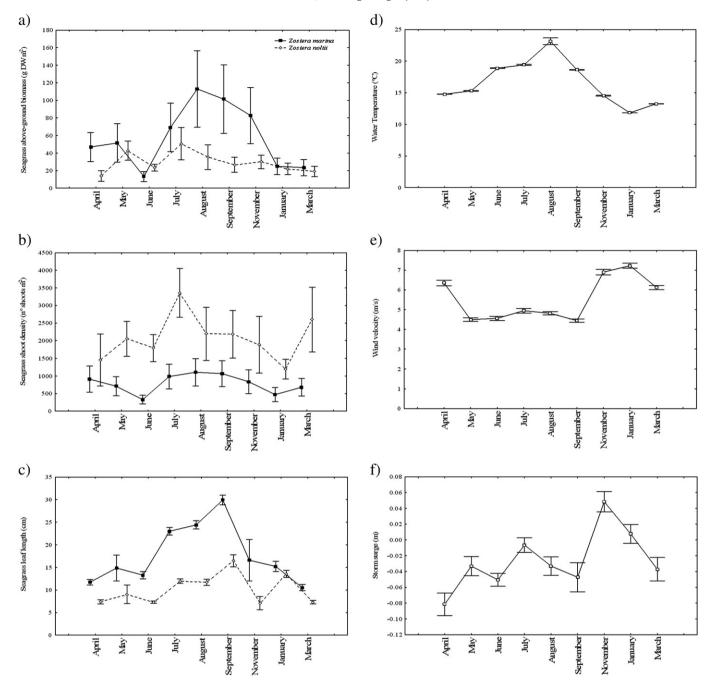


Fig. 3. (a) Biomass (g DW m⁻²), (b) shoot density (n° shoots m⁻²) and (c) leaf length (cm) (mean \pm standard error) of *Z. marina* and *Z. noltii* at the Bay of Santander in the period 2001–2002. Seasonal fluctuations of (d) water temperature (°C), (e) wind velocity (*m/s*) and (f) storm surge (*m*) for the same period are also shown.

of meadows is still limited, and more data is needed to understand how these species attenuate energy subjected to real conditions.

The influence of vegetation in sediment transport has been studied by several authors by means of field data. Garcia and Duarte (2001) demonstrated that *P. oceanica* fields decrease sediment erosion by reducing turbulence inside the meadow and restricting resuspension. Bos et al. (2007) showed that eelgrass beds contribute to sediment deposition in intertidal habitats pointing out the influence of seasonal behavior. Recently, Christianen et al. (2013) have highlighted the importance of the rhizoidal system in seabed stabilization. However, more in depth studies are needed to understand how different factors, such as standing biomass or rhizome biomass, influence processes like sediment transport and stabilization. Furthermore, the changes in flow patterns produced by seagrasses influence the transport processes. Granata et al. (2001) measured the particle and flow distribution within

seagrass meadows and identified three-dimensional transport patterns as the meadow acted as a bluff body diverting flow over it while producing secondary circulation patterns at its edge. These recirculation patterns strongly influence the sediment transport and it is important to put more efforts on measuring the flow inside and around vegetation fields in order to understand the erosion or accretion processes and the preference channels.

Due to the use of better-controlled conditions, laboratory measurements have been used to obtain measurements of wave transformation along submerged meadows in order to extract wave attenuation factors. Flume experiments have lead to generalizations based on simplified representation of both plants, mainly using plastic mimics, and hydrodynamic conditions, mainly by means of monochromatic waves. Only a few examples can be found with random wave conditions (i.e.: Stratigaki et al., 2011). Scale effects are also present at laboratory

experiments due to the difficulty in reproducing simultaneously realistic wave and plant conditions.

Early works were focused on determining wave decay using both plastic mimics, Asano et al. (1988) and real seagrasses, Fonseca and Callahan (1992). One of the main limitations of laboratory experiments is the mechanical simulation of the plant characteristics. Despite the importance of the Cauchy number, which relates the plant elastic force and inertia, Ghisalberti and Nepf (2002), introduced a new parameterization to preserve the plant characteristics when scaling. This issue represents an important limitation in generalizing laboratory experimental measurements because of the difficulty in finding materials, which preserve said characteristics.

In that line, Stratigaki et al. (2011) performed large scale measurements recording free surface elevation and the velocities inside and outside of a vegetation field made of artificial *P. oceanica*, attending to Ghisalberti and Nepf (2002) scaling. Higher attenuation values were observed for shallower conditions and denser vegetation fields. Although these studies give interesting results, more measurements will be needed to better understand the processes associated to flow-vegetation interaction. A better definition of flow characteristics inside and around the meadow together with three-dimensional studies will lead to a deeper understanding of wave damping. More recently, Luhar et al. (2010) detected the existence of a mean current in the direction of the wave propagation generated within the meadow formed by mimics and forced by a nonzero wave stress. The reduction of the wave-induced flow within the canopy meadow was found as a function of the ratio of the orbital wave excursion and blade spacing.

More recently, Paul et al. (2012) determined the effect of current velocity on wave attenuation for three different types of seagrass mimics, based on *Z. noltii* biomechanical properties. Their results showed that the presence of currents on top of the waves strongly reduces the wave attenuating capacity of the vegetation, and that the magnitude of this effect depends on shoot stiffness.

Several authors have considered the importance of vegetation mechanical properties. For example, Bouma et al. (2005) showed the value of plant stiffness in wave attenuation by comparing the salt marsh *Spartina anglica* with the seagrass *Z. noltii* and artificial vegetation made of different stiffness strips. All these studies clearly showed the importance of vegetation characteristics for their effect on hydrodynamic attenuation. The strong differences found between artificial and natural seagrasses in terms of quantitative results was shown by Fonseca and Koehl (2006) who demonstrated that wave decay differences were mostly due to the discrepancies in their mechanical properties.

There are more studies that determined the effects of vegetation on the flow, than vice versa, i.e. studies that determine the effects of flow on the vegetation. However, for a good understanding of sediment transport it is important to determine the drag forces exerted over the vegetation, in addition to the associated turbulence (Pujol et al., 2013). Drag forces are important, as they will determine the vegetation development and survival. Infantes et al. (2011) studied the combined effect of drag forces and erosion on seedling dislodgement from the substrata, in order to get a fundamental understanding of the seedling survival and of the role of hydrodynamics on the distribution of the most common seagrasses in the Mediterranean Sea (P. oceanica and C. nodosa). Marbà and Duarte (1994) also studied the response of C. nodosa to fluctuations in sediments depth, highlighting the sensibility of seagrasses to changes in its substrate, and Moriarty and Boon (1989) studied how seagrasses can change their own environment in terms of sediment trapping. There are still uncertainties according to the sediment stabilization provided by the different seagrasses species and this issue needs to be studied more in detail.

4.2. Numerical studies of coastal protection

The complexity of the flow structure when interacting with submerged vegetation has motivated also the numerical approach. According to the works existing in literature, a specific procedure is not followed for seagrasses, and it is analyzed in a similar way than other submerged vegetation. The difficulty in modeling numerically the wave interaction with submerged vegetation relies on the complexity of several features as the interaction of different time and spatial scales, the presence of turbulent flow, the non-linear flow characteristics or the representation of the plant behavior in the modeling, among others. The unaffordable computational cost derived from the implementation of a detailed description of the flow and bio-physical vegetation characteristics, such as stiffness or biomass, has motivated the use of simplified equations to model the momentum damping created by the submerged vegetation.

The use of numerical models to study wave interaction with submerged vegetation has been developed and linked to the improvement of wave modeling. Vegetation has been introduced in the numerical predictions using simplified models to determine wave energy reduction. Early works have been focused on conceptual models based on a bottom friction or bed roughness approaches (i.e. van Rijn, 1989) or based on modeling the damping created by simplified conditions, such as Dalrymple et al. (1984) where vegetation is considered as vertical cylinders on a constant, arbitrary water depth. The amount of energy dissipated by both approaches needs to be calibrated by means of measurements. However, the rigidity of the initial assumptions of the models does not ensure reliable results. A later expansion of the Dalrymple et al (1984) conceptual model was presented by Mendez and Losada (2004). The main advantage of Mendez and Losada (2004) model is the parameterization of the energy dissipation by means of a Morison-type equation, which includes the plant characteristics, the shoot density and the drag coefficient. The later was parameterized based on the Reynolds and Keulegan-Carpenter numbers using laboratory data.

Models based on potential flow theory were used first in order to get a more realistic representation of the flow field. Submerged vegetation was modeled by means of a momentum sink as a function of non-dimensional parameter called damping coefficient, which must be determined as a calibration factor. The coefficient modeled the viscous effects presented in the flow-plant interaction, which cannot be considered in the potential flow equations. Early works were based on regular non-breaking waves propagating over submerged meadows (Kobayashi et al., 1993). Mendez and Losada (2004) extended these studies to consider random breaking and non-breaking waves. Ota et al. (2004) later included wave and current interaction in the modeling. The strong limitation of the models based on potential flow theory lies on the fact that turbulent effects cannot be modeled and the prediction of wave transformation is limited to non broken waves.

Models based on depth-averaged equations were applied next. Suzuki et al. (2011) implemented the Mendez and Losada (2004) formulation in the full spectrum model SWAN (Simulating Waves Nearshore) to reproduce wave dissipation over vegetation fields. They included a vertical layer schematization for vegetation with variable vertical area but the vegetation was included based on its diameter, the number of vegetation elements per square meter and an empirical coefficient, which depends on wave characteristics. Therefore, the model does not address the issue of vegetation motion and flexibility, an aspect that is very important in seagrass species.

Boussinesq equations (Augustin et al., 2009) have been also used to improve the flow representation in the interaction between waves and plants and to solve transient effects. These models introduce non-linearity produced in the flow-vegetation interaction and improve the prediction of the wave transformation produced by the meadow. They account for vegetation effects as an additional friction inducing loss of momentum in the area occupied by the vegetation. The effect of the flow in the vegetation is modeled by means of a drag force as a function of the drag coefficient, which needs to be determined based on experimental measurements. Drag coefficient formulations presented by Mendez and Losada (2004) or Kobayashi et al. (1993)

are commonly used in this type of modeling to represent wave energy damping.

The use of models based on Navier–Stokes equations has become more popular in the last decade, due to the improvement of the computational resources. They can solve the whole flow structure, including the vertical flow component, and also can model non-linear effects and turbulence. Ikeda et al. (2001) presented a two dimensional approach including the wavy motion of the plants indentifying the monami produced over the canopy. Later, Li and Yan (2007) studied the wave–current–vegetation interaction using Reynolds Average Navier–Stokes (RANS) equations. Recently, Maza et al. (2013) presented a two dimensional approach based on RANS equations, introducing the coupled motion between waves and vegetation and a new turbulence closure model. These models can provide a very detailed representation of the flow, including the dynamics of the water inside the meadow. Moreover, they can account for the geometric and mechanical characteristics of the vegetation field.

Future efforts might enhance the integration of near field models, which solve the kinematics and dynamics inside the meadow and account for the bio-physical characteristics of each vegetation type, into far-field models to solve the whole problems at different scales. Furthermore, the sediment transport and stabilization due to these ecosystems is still understudied and must be covered in the future.

5. Threats to the coastal protection provided by seagrasses

Coastal areas occupied by seagrasses face anthropogenic and natural threats which at different spatial scales might be causing the decline of seagrass meadows (e.g. influencing their physiological, functional and structural state) and in turn the deterioration of the coastal defense abilities. Overall, the trends of seawater warming, increasing storms and sea level rise, together with the increasing population and anthropogenic threats in the coastal area may lead to rates of change too fast to allow seagrasses to adapt and maintain their coastal defense service (Orth et al., 2006).

At the local scale the decline can be mainly explained by anthropogenic threats related to the mechanical damage of the meadows (e.g. dredging), the deterioration of the water quality (e.g. nutrient, pollutants and suspended material release), or the introduction of invasive species (e.g. *Caulerpa taxifolia*). The observed consequence is an overall rapid seagrass loss over relatively short temporal scales, of years or decades (e.g. in the Mediterranean; Marbà et al., 2005), which has led the IUCN to include in the red list category the four European seagrass species as 'least concern' of extinction risk. Although some of these species may be locally threatened, this classification is primarily due to their large range sizes. The population trend of *Z. marina* and *Z. noltii*, for example, is declining in the Temperate North Atlantic bioregion, but is still widespread elsewhere and have large range sizes (Short et al., 2011; Fig. 1).

At the global scale climate change (increase in the water temperature, changes in wave regimes, extreme levels and sea level rise) represents an additional and decisive threat for the protection service provided by seagrasses. The increasing rate of global climate change seen in this century, and predicted to accelerate into the next, will have large potential impacts on habitat-forming species, such as seagrasses (Short and Neckles, 1999). Although European marine ecosystems are influenced by anthropogenic factors, every region has shown at least some changes that were most likely attributable to recent climate change (Philippart et al., 2011).

Climate-induced changes differ along a latitudinal gradient, although general expected changes and responses can be predicted. The increase in the water temperature will affect seagrass metabolism, which in turn may result in changes in seasonal and geographic patterns of abundance and distribution (Short and Neckles, 1999). As it was observed for *Zostera* spp. (Fig. 3), temperature warming might affect the seasonal fluctuations of the biological features involved in costal

defense capabilities (e.g. above-ground biomass, shoot density and leaf length). However, responses to seawater warming will depend on the individual thermal tolerances. For instance, in natural populations of the sensitive species *P. oceanica* might increase the mortality rates up to three times with a 3 °C increase in maximum annual seawater temperature (Marbá and Duarte, 2010). Likewise, the increase in intensity and frequency of storms may prevent the reestablishment of slow growing seagrasses such as *P. oceanica*, promoting plants uprooting or burying and increasing the risk of coastal erosion.

Finally, sea level rise will cause an increase in the water depth, with the consequent reduction of available light at the bed, the intrusion of seawater into estuaries and rivers and changes in the currents. The expected response of seagrass communities will be a reduction in the distribution area and changes in the structure and functional values. Despite the knowledge progresses gained so far, the prediction of seagrass responses under climate change is still difficult (Barbier et al., 2008).

To optimize the protection service supplied by seagrasses efforts must be focused on improving our understanding about how climatic and anthropogenic stressors translate into changes and responses in seagrasses. With that purpose, predictive mathematical models integrating climatic and ecosystem models have been developed (Philippart et al., 2011). Climatic models project where and how climate change will impact the coastal areas focusing on those factors with a direct effect on the habitat suitability (e.g. water column height or current velocity), while ecological models project the effect of climate change on seagrasses in terms of physiology and spatial distribution of species. Linking both models not only might provide a better understanding about spatial locations and mechanisms of climate-induced changes that will affect seagrasses, but also if such changes will be reversible. Accordingly, future planning strategies should be supported by these predictive tools in order to deal with climate change consequences on coastal areas, seagrass responses and defense provided. Nevertheless, the scientific research in this field still shows important gaps (e.g. how climatic and anthropogenic stressors translate into seagrasses responses) and it is necessary to improve the knowledge and predictive capacity incorporating other anthropogenic stressor and interactions.

6. Adaptation measures to improve the coastal protection provided by seagrasses

Adaptation measures are the approaches to amend the possible loss of protection abilities caused by the decline of seagrasses by natural or anthropogenic threats and the increase of the coastal risk by flooding and erosion

Coastal risk (e.g. flooding and erosion) can be reduced by artificial measures such as construction of new structures, beach nourishment or coastal realignment. An additional solution to preserve and enhance the coastal protection service against the climate change effects is the use of hard structures, such as man-made reef mimics, oyster domes or submerged breakwaters (Meyer et al., 1997; Piazza et al., 2005; Swann, 2008). This type of structures attenuates the increasing hydrodynamic forcing, reducing the energy level that arises to the seagrass meadow. Another approach to protect the coast is the combination of artificial elements (e.g. breakwaters and seawalls) with vegetation fields (ecological engineering solutions). Such combination between hard structures and natural ecosystems arises from the necessity of reducing the environmental impacts produced by the massive construction along the shoreline (Bergen et al., 2001; Schulze, 1996). Some experiences have been obtained by using vegetation with high energy dissipation rates, such as mangroves (Tusinski, 2012) or willow forests (Borsje et al., 2011), but no experiences have quantified the effects of positive feedbacks on seagrass performance.

Alternatives to artificial actions include (1) the reduction of human pressure on existing ecosystems, to preserve their extension and health, and (2) the adaptation of seagrass beds to climate change, to ensure

defense services are maintained or improved. Few studies have related coastal protection to habitats health, but it makes sense that stressed organisms with lower biomass and shoot density may lead to lower coastal protection capabilities (Koch et al., 2009). Thus, healthy seagrasses can be assumed to be better adapted to global changes and to improve the efficiency of the coastal protection offered (Björk et al., 2008). The health of seagrass beds depend on many and interconnected local environmental factors which cannot usually be controlled directly, but indirectly through the anthropogenic activities responsible of nutrients, pollutants and suspended material release (e.g. Dredging; Erftemeijer and Lewis, 2006).

Protection services offered by seagrasses may be incomplete without the ecological interactions with other ecosystem engineer species also contributing and enhancing coastal protection (Short et al., 2011). Among other factors, wave attenuation is a function of the amount of plant and sedentary animal material obstructing the water column and the water depth (Coops et al., 1996). As a result, defense of any coastal interface system may rely on the cumulative effect imposed by biotic and abiotic characteristics (e.g. geomorphology and bathymetry) of the coastal zone (Koch et al., 2009). Along temperate European coasts not only plant cover in ecosystems such as seagrass beds, saltmarshes and dunes, is able to reduce current velocities, dampen waves and trap sediment, but mussel beds, oyster beds and Sabellaria reefs can have similar effects on sediment and currents on a smaller scale (Alongi, 2008; Barbier et al., 2011; Borsje et al., 2011; Koch et al., 2009).

The last option is the restoration of bare areas. Seagrass die-off tends to be rapid, whereas natural recovery of disturbed seagrass habitats is comparatively slow (Lee and Park, 2008). As a result, in the last decades numerous restoration projects through transplanting seagrasses have been attempted (Bastyan and Cambridge, 2008; Fonseca et al., 1994; Lee and Park, 2008; Short et al., 2002; Thorhaug, 1987; West et al., 1990; Zimmerman et al., 1995). Traditionally, restoration projects have been planned at relatively small scales (<1 ha), but since managers become aware of the value of seagrass meadows in the coastal protection, the interest on larger-scale transplantation programs is growing (Orth et al., 2006). Restoration actions are determined by the insufficient knowledge about the biology of the plants, the uncertainties in the techniques and the time scales. Worldwide the success of seagrass transplantation and restoration is uncertain and the experiences among species vary enormously. Z. marina is the species most widely transplanted. The survival rates vary considerably with the planting method, but a compilation of 53 planting experiences in the USA showed a mean planting unit survival of 42% after one year. Likewise, the slow growth rates of *P. oceanica* may cause problems in sufficient source material for transplantation, but pilot studies showed survival rates of 70% after 3 years (Christensen et al., 2004).

7. Conclusions and knowledge gaps

Throughout this contribution it has been shown that the role played by seagrasses on the coastal protection should be actively included and not be overlooked in coastal planning. The literature provides sufficient evidences about the capacity of submerged aquatic vegetation to supply coastal protection services and seagrasses is the largest submerged ecosystem protected in Europe. It has been shown that science is strongly advancing to evaluate processes, efficiency and parameters that affect the defense service provided. However, there are still many uncertainties in the characterization and quantification of the protection offered by seagrasses, which demands greater attention from science if it is to be applied as a real adaptation option. The main conclusion achieved is that seagrass meadows cannot protect shorelines in every location and/or scenario. The efficiency of the protection depends largely on the incident energy flux, density, standing biomass and plant stiffness. The optimal conditions for enhancing the defense provided might be achieved at shallow waters and low wave energy environments, with high interaction surface, in the vertical and horizontal dimension, between water flow and seagrasses, but less so when hydrodynamic conditions are more severe. Likewise, the most favorable protection might be offered by large, long living and slow growing seagrass species, with biomass being largely independent of seasonal fluctuations and with the maximum standing biomass reached under the highest hydrodynamics forcing.

From the review performed a number of knowledge gaps have been identified.

- There is a need to examine the flow-vegetation interaction with models integrating near field into far field models in order to be able to reproduce problems at different spatial and temporal scales.
- A better characterization of how seagrass species characteristics (e.g. biomass, shoot density, stiffness or morphology) influence the dynamics involved in wave and current attenuation and sediment transport is required.
- There is also a need for specific field data that enable establishing a wider geographical and ecological database relating plant properties to hydrodynamic conditions, relevant to bio-physical interactions in coastal seagrass meadows.
- There is a clear knowledge gap on the performance of coastal defense systems that combine seagrasses with artificial elements (e.g. breakwater or seawalls).
- There is a significant need to develop tools to predict the effect of climate change on seagrasses structure and functioning.

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