Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Review

Seascape ecology in *Posidonia oceanica* seagrass meadows: Linking structure and ecological processes for management

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ABSTRACT

Seagrass meadows constitute marine habitats in shallow water temperate and tropical coastal areas worldwide that have a high ecological and economic importance. Amongst the 60 or so seagrass species, the endemic Mediterranean species *Posidonia oceanica* forms meadows that are arguably the most important shallow water coastal habitat in the region but which are subjected to high anthropogenic pressures. Because of the relatively large size of the plant, the meadows formed by this seagrass have high architectural and morphological complexity, which results in different morphotypes or seascapes. While numerous studies of *P. oceanica* architectural characteristics for continuous meadows of the seagrass are available, few works have addressed seascape ecological features and the influence of environmental factors (natural and anthropogenic) thereon. In the present review, we give an overview of *P. oceanica* meadow architectural and morphological characteristics and how these contribute to Mediterranean landscapes and seascapes. Studies addressing the influence of natural and anthropogenic factors on morphometric features of different meadow types and landscape ecological characteristics of *P. oceanica* habitat are also reviewed, as well as their influence on ecosystem processes. Finally, by considering the available data and tools for seascape studies, we present a discussion on methods to assess seagrass seascapes within the framework of coastal management. Our review highlights several gaps in *P. oceanica* seascape ecology knowledge such as the lack of data on the spatial distribution of this engineer species, and the possibility to use modern techniques and procedures for analysing structural and ecosystemic data.

1. Introduction

A landscape can be defined as a shifting arrangement of biotic structures and the resulting mosaic of patches (Fig. 1) (Robbins and Bell, 1994). In turn, the patches are surrounded by a border called an 'edge' (Fig. 1), which delimits different adjacent habitats (Pickett and Cadenasso, 1995). The whole structure is embedded within a matrix which plays a major role in connecting patches, thus ensuring landscape functioning (Fig. 1) (Forman and Godron, 1986). Within this context, landscape (or 'seascape' when dealing with marine habitats) ecologists aim to study the structure (morphology and size), function (functional ecology) and changes (evolution) of these biotic systems (Turner, 1989). Moreover, recent advances have identified two ways to consider the study of seascape ecology: one similar to landscape ecology for coastal ecosystems; one designed for pelagic ecosystems and their specific spatial and temporal characteristics (Kavanaugh et al., 2016; Pittman, 2017).

The definition of a *P. oceanica* seascape (and more generally of any seagrass seascape) will vary according to substratum type *e.g.* sand,

bare mat and rock (Pagès et al., 2014), while the meadows themselves also comprise a matrix (Abadie et al., 2015). Seagrass habitat structure can be viewed at various levels – from within-meadow architectural features to gross meadow morphology; the latter ranging from continuous to patchy. The function of seagrass seascapes includes the influence of meadow structure on the associated biota. Lastly, change corresponds to the evolution over time of seagrass habitat structure and/or function. All these aspects can be studied at various spatial scales, from a few centimetres to hundreds of kilometres. Hereafter, we use 'small scale' in the context of an area covering less than 1 km^2, and 'large scale' within the context of an area larger than 10 km^2.

The practical value of data from seascape studies is their use to manage marine habitats and to model their evolution, taking into account the ecosystems' key species (Boström et al., 2011). Although this approach is commonly used in terrestrial ecosystems management and conservation (Turner, 1989; Zonneveld, 1995), it is seldom applied to coastal seascapes (Li and Mander, 2009), including seagrass meadows (Pittman et al., 2011). In part, this results from the lack of available data on the link between the occurrence and distribution of species
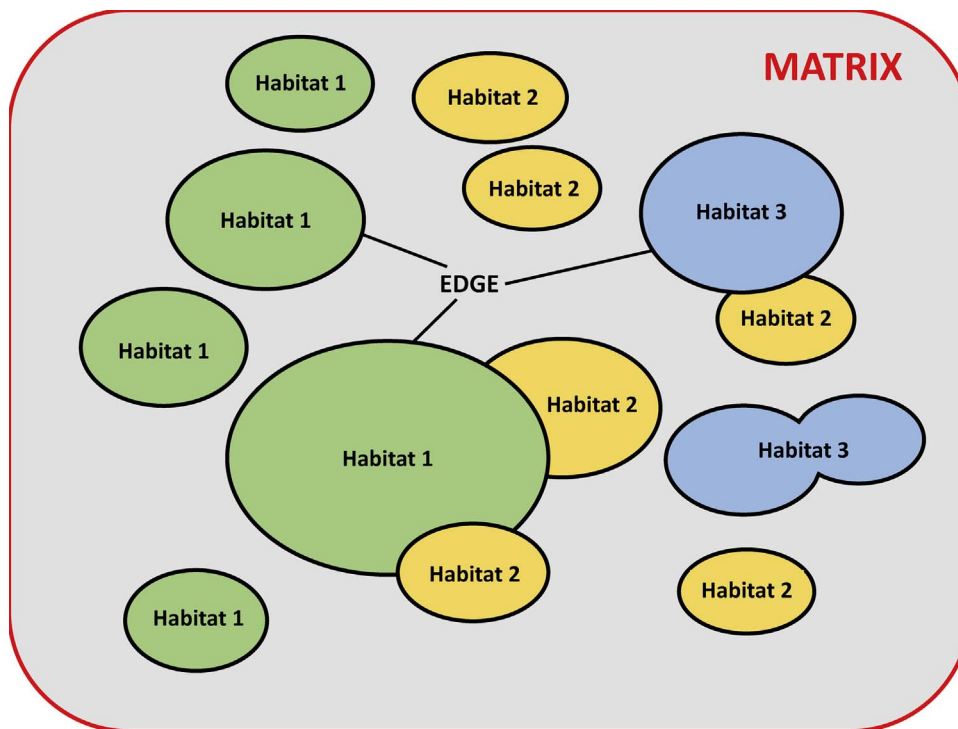
Fig. 1. Conceptual representation of different habitat compartments forming a landscape (or seascape).

associated with seagrass habitat and seagrass meadow structure (Boström et al., 2006).

The present work aims to highlight the importance of the seascape approach in the management of seagrass meadows through use of a well-documented species as example: *P. oceanica*. In the present work, we review previous seagrass seascape studies to: (1) highlight the main architectural characteristics of different *P. oceanica* meadow types; (2) identify the influence of main natural and anthropogenic factors on *P. oceanica* habitat; (3) describe the role played by *P. oceanica* seascapes on the associated biota; and (4) evaluate the contribution of *P. oceanica* meadows to the Mediterranean seascape. Finally, we identify gaps in knowledge and propose future work within the field of seascape ecology and management, as applied to *P. oceanica* and other seagrass habitats.

2. Bibliographical research

A bibliographical search of seagrass seascape studies was first undertaken without restricting to any one seagrass species. References to *in situ* studies were extracted from previous reviews concerning seagrass seascapes (Boström et al., 2006, 2011; Connolly and Hindell, 2006; Grober-Dunsmore et al., 2009; Heck et al., 2008; Horinouchi, 2007; Kendrick et al., 2005a; Vacchi et al., 2017). To complete this first approach, a search was then performed using the Scopus and Google Scholar data bases, using the keywords 'seagrass'; 'landscape'; 'seascape'; 'patch'; 'structure' and 'architecture'.

All references were then classified according to the field of study in seascape ecology, referring to the subjects of interest defined by Turner (1989), i.e. the structure (S), function (F) and changes (C). Furthermore, the method and spatial scale of each study was addressed by using a qualitative symbology scheme (Table 1).

3. *Posidonia oceanica* seascape characteristics

3.1. Available literature on Posidonia oceanica seascape ecology

The first work that makes reference to *P. oceanica* seascape was undertaken by Molinier and Picard (1952) along the French

Table 1
Symbology for sampling methods and spatial scales considered in seagrass meadow studies used in the present bibliographical search.

	Area	Symbol
Method		
Quadrats and sampling spots	Tens of cm^2	Q
Transects (scuba diving, video, trawling)	Hundreds of m^2	T
Small patches	Less than 10 m^2	SP
Large patches	Tens of m^2	LP
Mapping (cartography, grid model)	Exhaustive	M
Area studied		
Small scale	< 1 km^2	SSS
Medium scale	1–10 km^2	MSS
Large scale	> 10 km^2	LSS

Mediterranean Coast. This study described 'intermatte' features, *i.e.* sand patches or channels present amongst the *P. oceanica* meadows and presumably resulting from the effects of bottom currents that are a residual product of wave action. Following this relatively early study, it was not before 1998 that the number of seagrass seascape studies started to increase (Fig. 2), reaching a total of 157 scientific works to date. The main species studied are *Zostera marina* and *Posidonia oceanica*; 23% and 34% of all published works respectively. When considering the total number of works reviewed (Fig. 3), studies carried out at the small spatial scale (SSS) are more numerous and comprise 53%. However, studies carried out at large spatial scale (LSS) increased in number from the mid-2000s, reaching 30% of the total published works in recent years (Fig. 3). It is noteworthy that the first work undertaken at a large spatial scale was focused on *P. oceanica* (Pasqualini et al., 1998). When considering study methods, mapping (M) at various spatial scales appears to be the most popular methodology to study seagrass seascapes (40%), followed by quadrat sampling and discrete sampling (Q-DS) techniques, which represent 27% of published works (Fig. 4). Details of the whole bibliographical search are available in the supplementary material Table SM1.
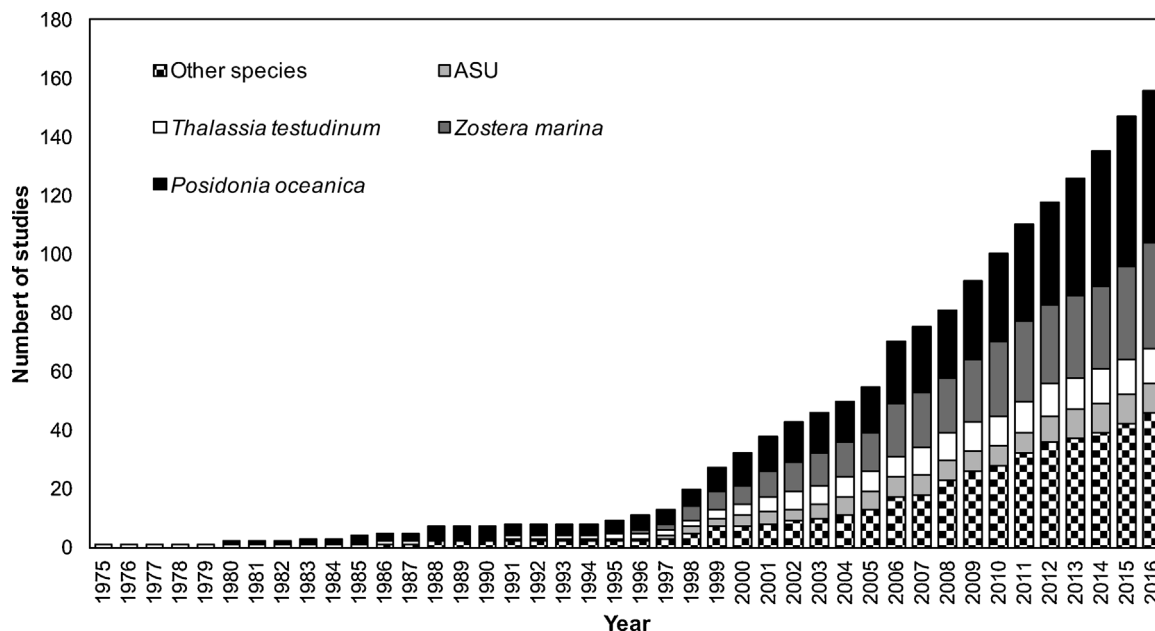
Fig. 2. Cumulative number of studies concerning seagrass seascape ecology published from 1975 to 2016. ASU: artificial seagrass unit.

3.2. Posidonia oceanica within-meadow architectural characteristics

Development of heterogeneous *P. oceanica* seascapes at the large spatial scale starts at the genetic level. More specifically, genetic diversity is correlated with meadow shoot density; the slow stolonization rate (asexual reproductive process of a *P. oceanica* shoot) over a long temporal scale leading to an increase of shoot density at the centre of isolated patches (Zupo et al., 2006a). The separation of two distinct branches on a single *P. oceanica* rhizome thus depends on an internal biological clock (Molenaar et al., 2000). After the development of new shoots, their orientation (orthotropic or plagiotropic) can be reversed (Molenaar et al., 2000) in order to adapt to change in environmental factors, such as sedimentation or the availability of unvegetated substrata that can be colonized. No competition is observed between the new shoots and no increase in leaf size is observed when shoot density decreases (Panayotidis et al., 1981). However, an opposite phenomenon in the growth characteristics of the plant is observed when taking into account the sediments chemistry (e.g. pH, nutrients concentrations, redox potential) (Gobert, 2002). Differences in morphology, growth rate, leaf length and density mainly occur at small spatial scales (Balestri et al., 2003; Borg et al., 2005; Zupo et al., 2006b). Under disturbances, Marbà et al. (1996) reported a shoot recruitment rate of *P. oceanica* that was lower than the mortality rate, thus leading to a slowly decreasing shoot density.

Specific features of shoots making up *P. oceanica* seascapes that vary at a very small scale, i.e. $< 1\,m^2$, lead to changes in shoot density at a larger spatial scale. This assertion has been verified at the spatial scale of hundreds of meters by Gobert et al. (2003) who noted the largest variation of meadow structure between 8 and 12 m depth, and which were attributed to some internal plant mechanism. Borg et al. (2005), who compared the within-meadow structure of reticulate and continuous meadows, observed no differences between the two meadow types over different spatial scales. Differences in shoot density will lead to parts of a seagrass meadow that have less resistance against erosive
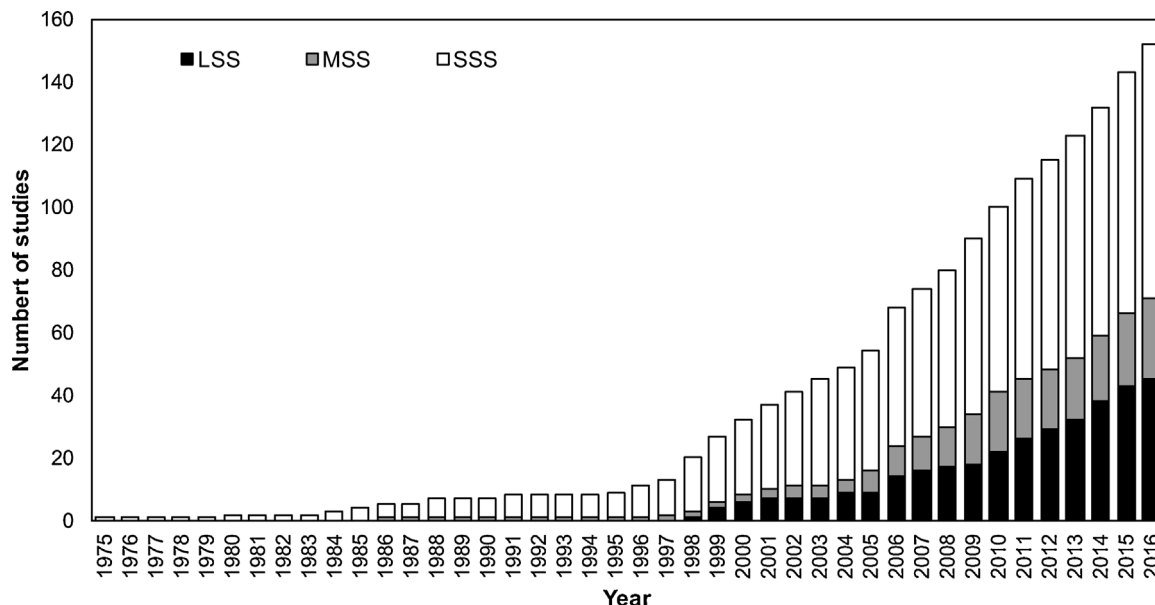

Fig. 3. Cumulative number of studies, categorized according to spatial scale addressed, published from 1975 to 2016. LSS: large scale; MSS: medium scale; SSS: small scale.
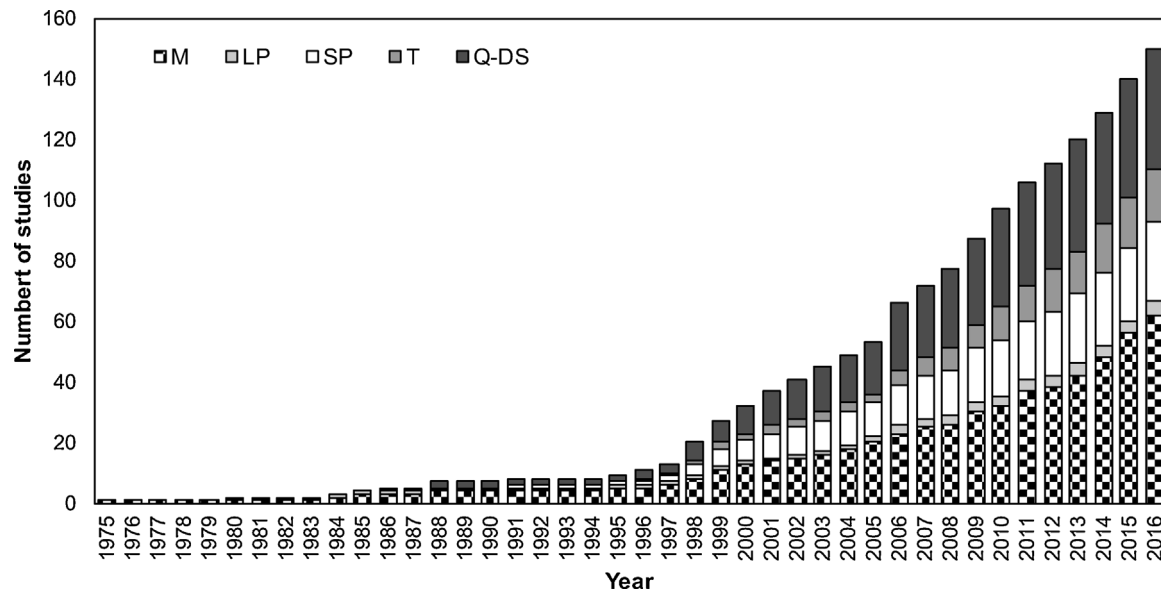
Fig. 4. Cumulative number of studies categorized according to study methodology, published from 1975 to 2016. SP: Small Patch; LP: Large Patch; M: Mapping; T: Transect; Q-DS: Quadrat-Discrete Sampling.

forces (*e.g.* sea currents and physical damage from anthropogenic activities), leading to the generation of patches at the seascape scale (Panayotidis et al., 1981) and development of different meadow morphotypes.

Far from being a flat and homogenous structure, *P. oceanica* meadows contribute to a seascape that is vertically structured because of their complex within-meadow architectural features. The leaf canopy acts as a trap of both organic and inorganic particles, with the leaves preventing their resuspension (Dauby et al., 1995). Gacia and Duarte (2001) assessed resuspension of particles within a *P. oceanica* meadow and noted that this was lower by a factor of 3 compared with a bare sediment bottom. The particle retention rate is increased by a factor of 5 during periods of exposure to erosion (*e.g.* during winter storms) (Gacia et al., 1999). Accumulation of the trapped sediment particle results in an elevation of the seabed, leading to corresponding vertical growth of *P. oceanica* rhizomes (Boudouresque et al., 1983; Boudouresque and Meinesz, 1982). The complex formed by sediments, living/dead roots and rhizomes is called "matte" (Boudouresque and Jeudy De Grissac, 1983; Gobert et al., 2006). This structural component, which can be several meters thick (López-Sáez et al., 2009), serves as an important carbon store (Mateo et al., 1997; Pedersen et al., 2011) while its dynamics are strongly linked to the seascape structure of *P. oceanica* meadows. Thus, the rhizome layer is sandwiched between the matte and leaf canopy.

3.3. Impacts of natural and anthropogenic factors on Posidonia oceanica seascapes and within bed architecture

Posidonia oceanica seascapes are strongly influenced by both natural and anthropogenic factors which determine their shape, and thus function, at various spatial scales.

Among natural factors, water movement, such as that associated with waves and currents, appears to be a main factor influencing the *P. oceanica* meadow structure at both within-meadow and seascape scales. However, this cannot always be verified as shown by Borg et al. (2009) who observed that high patchiness was not always linked with a high exposure.

At shallow water depths, strong bottom currents and the mechanical action generated by wave breaking prevent establishment of *P. oceanica* meadows. This has been confirmed by Infantes et al. (2009) who report that a current velocity higher than $40 \, cm \, s^{-1}$ compromises colonization

by the plant. Similarly, Pace et al. (2017) show that at shallow depth (6–11 m depth), high energy wave climate leads to an increase of meadow patchiness and a decrease in architectural complexity. At greater water depths, even if negligible, currents derived from wave energy result in a decrease of meadow cover resulting in the generation of patches of different bottom type (bare matte or sandy bottom) (Abadie et al., 2017; Gobert et al., 2016; Vacchi et al., 2010). Furthermore, *P. oceanica* meadows enhance sediment stabilization of sandy patches present in their vicinity (Vacchi et al., 2017). At the large spatial scale, sandy patches intermixed within a *P. oceanica* meadow are clearly recognizable, as shown by side scan sonar images, and can occupy from 2% to 16% of the total seagrass meadow area (Abadie et al., 2015; Clabaut et al., 2014; Pasqualini et al., 2000; Pasqualini et al., 1999).

When considering smaller areas, *e.g.* a small bay (< 1 km² in size), other causes of meadow fragmentation, such as those resulting from wave action generated by high winds, are noted. As a result, sandy patches called "return river" (Boudouresque et al., 2012) can be generated within a *P. oceanica* meadow, the nature of which would depend on orientation of the coastal area concerned to the main winds influencing it (Boudouresque and Meinesz, 1982). Furthermore, such a situation can lead to an increase in the number of sandy patches present within a meadow (Abadie et al., 2015; Meinesz et al., 1988).

At the small spatial scale (*i.e.* several square meters) the architectural features of a *P. oceanica* meadows exhibit high heterogeneity because of several local natural factors such as nutrient availability, granulometry and pH (Borg et al., 2005; Gobert et al., 2003). External abiotic factors are coupled with internal ones, as well as structural features to lead to development of particular *P. oceanica* seascapes; one example is that described by Boudouresque et al. (1985) concerning the formation of a 'barrier reef', which results from long term sedimentation and the vertical growth rate of the plant (Fig. 5). In the same way, variation in horizontal growth of *P. oceanica* rhizomes leads to a heterogeneous seascape. This observation is based on a long term simulation which revealed colonization, over a period of 600 years, of an area measuring 0.3 ha, with the seascape being slowly modified throughout this period (Kendrick et al., 2005b). This process may not be a linearly dynamic one, with recruitment increasing with an increase in *P. oceanica* patch size (Almela et al., 2008). Seafloor morphology, as well as geology (*e.g.* sand, rock), also play an important role in determining seascape heterogeneity (Montefalcone et al., 2016). At the
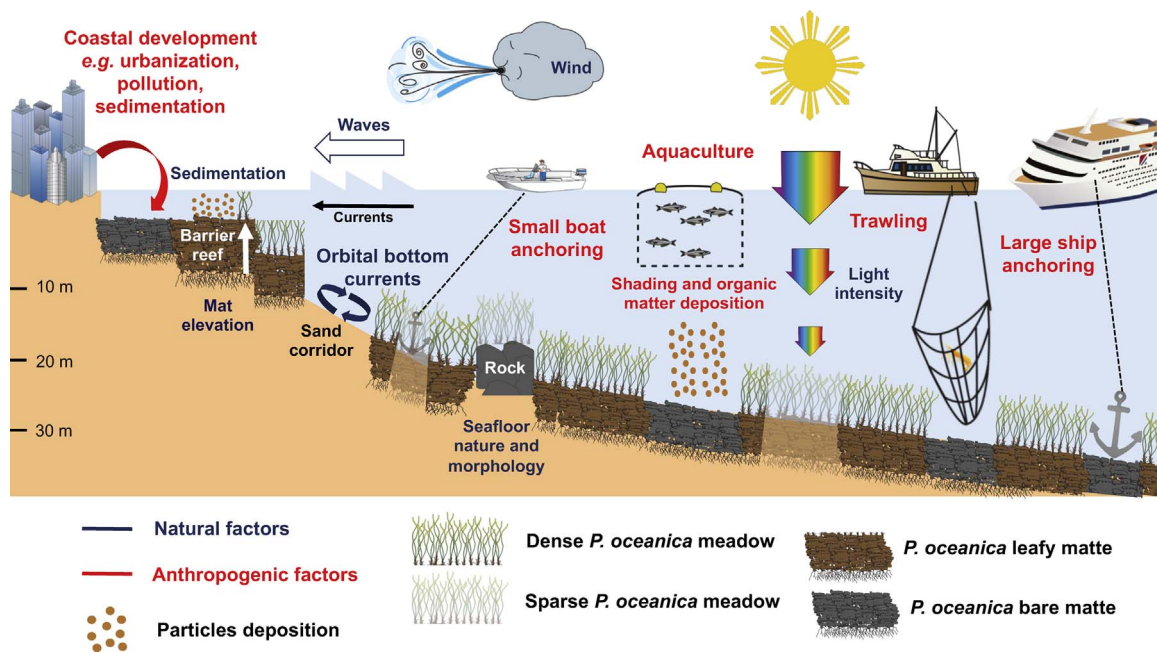
Fig. 5. Schematic diagram showing natural and anthropogenic factors that influence a *P. oceanica* seascape. The scale on the left indicates water depth.

level of shoot density and plant growth dynamics, local environmental factors may lead to a high degree of patchiness which is manifested as nestlike patterns (Zupo et al., 2006b). Similarly, decreased light intensity may lead to alteration of seascape micro-structure (see Fig. 5), as for example demonstrated by Dalla Via et al. (1998) who recorded a decrease of 72% in shoot density between a water depth of 3 m and 10 m.

Human activities, such as coastal development, trawling, anchoring, fish farms, are well known to directly modify *P. oceanica* meadow structure at all depths (Boudouresque et al., 2009; Giakoumi et al., 2015), but such effects are less evident within the 35–43 m bathymetric range (Pasqualini et al., 1998). As in the case of naturally-occurring patches of the seagrass, patches resulting from anthropogenic activities can be clearly identified at a large spatial scale according to their size and shape (Abadie et al., 2015; Clabaut et al., 2014; Pasqualini et al., 1999).

In places characterized by intense human activities, anthropogenic impacts on *P. oceanica* habitat result in higher levels of fragmentation compared to natural processes (Leriche et al., 2006; Montefalcone et al., 2010b). However, in areas characterized by moderate anthropogenic pressures, *P. oceanica* seascapes have a relatively low percentage of patches that result from human impact. For example, in Corsica (France), patches resulting from anthropogenic impact comprise only a maximum 6% of the total seagrass area and no further significant regression has been recorded (Abadie et al., 2015; Bonacorsi et al., 2013).

In general, increased levels of anthropogenic impact favours the development of bare matte areas (Tamburello et al., 2012), leading to decreased *P. oceanica* patch size and edge length (Nowell, 2014). Anthropogenic impacts have different temporal scales of action, resulting in the creation of bare matte patches within the *P. oceanica* matrix. In the long term, if the adverse activities continue at the same intensity, a shift in the seagrass meadow matrix can occur, resulting in areas with bare sand or dead matte (Ardizzone et al., 2006). Among the human activities that operate over a long period to eventually lead to fragmentation of meadows, hence patch generation, are pressures linked with coastal development (pollution and high rates of sediment deposition, as well as urban expansion; see Fig. 5), will first lead to a decrease in shoot density and then to fragmentation of a *P. oceanica* meadow (Montefalcone et al., 2007, 2010b; Rountos et al., 2012). On the other hand, anthropogenic activities causing direct physical damage

(*e.g.* boat anchoring, trawling, explosives) immediately lead to seagrass meadow fragmentation and to formation of patches (Fig. 5), thus modifying the seascape configuration (Kiparissis et al., 2011; Meinesz and Lefèvre, 1984; Okudan et al., 2011). Changes in the substratum's biogeochemistry as a result of mechanical damage can lead to intrusion of toxic compounds (e.g. hydrogen sulphide), which limit *P. oceanica* growth and meadow development (Abadie et al., 2016).

3.4. Influence of P. oceanica seascapes on the associated biota

As for meadows formed by other seagrass species, the occurrence and distribution of biota associated with a *P. oceanica* seascapes are mainly influenced by substratum type and meadow architecture (Boström et al., 2011). The transition between one habitat type and an adjacent different one and that delineating a patch of a given habitat type is called the 'edge' or 'ecotone' (Forman, 1995). For several species, their abundance tends to be higher at such junction between two different habitats; a phenomenon termed the 'edge effect' (Odum and Barrett, 1971). Edge effects have been given considerable attention in recent studies within seascape ecology that have been aimed at linking meadow or patch structure to the species' distribution, with emphasis on a particular taxon, assemblage, or functional trait (Boström et al., 2006).

Benthic communities are known to change according to environmental characteristics, including substratum type, and anthropogenic influences (Borja et al., 2003; Eagle, 1975). This has been confirmed in studies of interactions between *P. oceanica* meadows and bare sediment bottoms, the results of which have indicated a higher diversity and abundance of epifauna at the edge of a seagrass meadow (Fig. 6). For example, mysids prefer the meadow edge, while other taxa show no specific preference for location within a habitat except at the level of the species (Sánchez-Jerez et al., 1999). Settlement of non-mobile benthic species like *Pinna nobilis* Linnaeus also shows a strong edge effect, with more than half of the bivalve population found at the border of a *P. oceanica* meadow (Coppa et al., 2010). Therefore, the occurrence and distribution of *P. nobilis* appears to be greatly influenced by seagrass meadow form and structure within a seascape.

Amongst the substrata associated with *P. oceanica* meadows, dead matte (resulting from both natural or anthropogenic factors), although classically considered as an impoverished substratum in terms of the
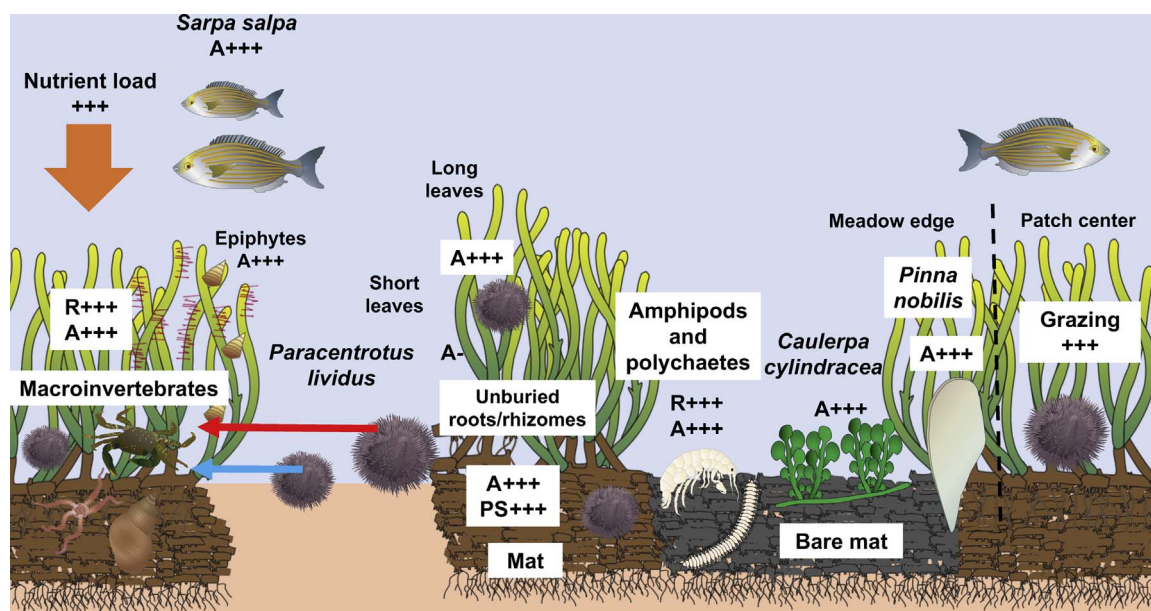
Fig. 6. Schematic diagram showing factors that influence the occurrence and distribution of species associated with a *P. oceanica* seascape. R: specific richness; A: abundance; PS: post-settlement.

biota it supports, have been noted to support a similar species richness compared with living matte (Fig. 6). For example, Borg et al. (2006) highlighted differences in the assemblage structure of macro-invertebrates associated with naturally-occurring dead matte; a higher abundance of the amphipods *Leptocheirus guttatus* Grube and *Maera grossimana* Montagu, and the polychaeta *Nereis rava* Ehlers were recorded from this substratum type compared to living matte of healthy *P. oceanica* meadows. (Coppa et al., 2010) noted that populations of the bivalve *P. nobilis* have a higher density on bare matte (Fig. 6) compared to living matte of *P. oceanica* and bare sand. In the case of dead matte resulting from anthropogenic activities such as illegal trawling, differences in population densities at microscale level (0.1–1 m) have been recorded for amphipods and isopods when compared to the same groups associated with living matte (Sánchez-Jerez and Ramos Esplá, 1996).

In areas where a habitat is under the influence of nutrient enrichment, such as *P. oceanica* meadows located near fish farms, workers *e.g.* Dimech et al. (2002) have observed a localized increase in species richness and abundance as a result of increased productivity (Fig. 6); this despite a change in meadow structure which was evident by lower leaf length and shoot density of *P. oceanica* located near the fish farm. Therefore, meadow structure alone does not determine the occurrence and distribution of species associated with the seagrass, and other factors can modify the *P. oceanica* seascapes' function. Studies have also indicated that small modifications of seagrass meadow structure may not have an appreciable influence on the associated macroinvertebrate assemblages but these are more influenced by other factors such as epiphyte biomass and sediment grain size (Borg et al., 2010).

The most studied functional aspect of *P. oceanica* seascapes is that concerning grazing of the leaf canopy by herbivores. The largest grazers are sea urchins *Paracentrotus lividus* Lamarck and the saupe *Sarpa salpa* Linnaeus, which attract attention as a result of their ability to consume and digest large amounts of *P. oceanica* tissue (Peirano et al., 2001).

Study of the occurrence and distribution of benthic species often includes an assessment of their settlement preferences within the considered habitat. In *P. oceanica* seascapes, Prado et al. (2009) observed that one-year cohort individuals of *P. lividus* tend to prefer *P. oceanica* matte as post-settlement habitat (Fig. 6), and absence of this substratum led to 100% non-survival of the post-settled individuals. Still, this process would depend on the individuals' proximity to *P. oceanica*

habitat despite their ability to move toward a meadow (Fig. 6). Furthermore, the process does not depend on seagrass patch size (Ceccherelli et al., 2009), suggesting that even young individuals can reach the matte. In this way, the abundance of *P. lividus* increases on the seagrass matte at the edge of a meadow (Pinna et al., 2013) where they are protected from fish predation by the longer leaves, as well as by the unburied portion of the rhizome layer (Farina et al., 2009).

When comparing the functional compartment of *P. oceanica* grazers, namely *S. salpa*, *P. lividus* and amphipods, all of which are motile consumers, it is not only the influence of meadow structure on their distribution which is useful for study but also their impact on seascape characteristics. For example, at the level of influence of seagrass meadow structure, Pagès et al. (2014) show that *P. lividus* and *S. salpa* increase their grazing pressure at the centre of *P. oceanica* patches rather that at their edge (Fig. 6). Such findings suggest that *P. oceanica* patches established on a rocky bottom are more subject to grazing than those present on a sandy bottom. The increase in grazing pressure, combined with natural fragmentation of the seagrass meadows, leads to loss of *P. oceanica* primary production (Gera et al., 2013).

The natural and human-induced heterogeneity of *P. oceanica* seascapes, for example where sand and bare matte patches are introduced within meadows of the seagrass, provide substrata for colonization by invasive and fast-growing non-indigenous species. In the Mediterranean Sea, this phenomenon has been especially studied for Chlorobionta of the genus *Caulerpa*. These species are able to substitute *P. oceanica* faster than native species, leading to a higher rate of fragmentation of meadows of the seagrass (Montefalcone et al., 2010a).

The first non-native species historically studied for its interaction with *P. oceanica* meadows is *Caulerpa taxifolia* (Vahl) C. Agardh; a circumtropical Chlorobionta member that was accidentally introduced in the north-western Mediterranean Sea (Jaubert et al., 2003). De Villèle and Verlaque (1995) observed that *C. taxifolia* established within a *P. oceanica* meadow causes demise of the seagrass, although plant to mortality decreases with an increase in shoot density. The higher *P. oceanica* shoot density has a shading effect on *C. taxifolia* blades, leading to a lower photosynthetic capacity and, hence, size of the alga and, by extension its colonization capacity (Ceccherelli and Cinelli, 1999). Based on several years of observation, Jaubert et al. (1999) reported no long-term impact of this alien alga on *P. oceanica* meadows invaded by this species. However, later it transpired that other

competitive processes between *P. oceanica* and *C. taxifolia* do occur through the release of chemical compounds into the substratum, as these lead to changes in the growth pattern and structural development of the seagrass (Pergent et al., 2008). Currently, *C. taxifolia* has almost disappeared from sites previously colonized, its regression being ascribed to a decrease of its dispersion capacity (Montefalcone et al., 2015).

Another non-indigenous Chlorobionta species, *Caulerpa cylindracea* Sonder, originates from south-western Australia; its presence has been noted in the Mediterranean Sea since 1990 (Klein and Verlaque, 2008). This species tends to prefer patches of bare matte within a *P. oceanica* seascape (Fig. 6) rather than bare sediment and rocky bottoms (Katsanevakis et al., 2010). *C. cylindracea* also colonizes impacted habitats, such as those exposed to trawling activities, including *P. oceanica* meadows affected by the activity (Kiparissis et al., 2011). *C. cylindracea* has been noted to be unable to penetrate dense *P. oceanica* meadows and only remains established along their edges (Ceccherelli et al., 2000).

3.5. Connectivity of Posidonia oceanica meadows with the Mediterranean seascape

Landscape/seascape connectivity is well studied in tropical areas which support a triangular network of mangroves, coral reefs and seagrass meadows (Berkström et al., 2012; Grober-Dunsmore et al., 2009). Although connectivity between marine and terrestrial Mediterranean habitats has not been studies much at a large spatial scale, merging several isolated works provides an insight into the role played by *P. oceanica* meadows (Fig. 7). Through export of primary production (Boudouresque et al., 2015) and their influence on water movement (Vacchi et al., 2017), *P. oceanica* meadows interact with other habitats, both marine and terrestrial (Heck et al., 2008), thus connecting with the whole Mediterranean coastal landscape and seascape.

A *Posidonia oceanica* seascape is mainly linked with terrestrial habitats at the level of beaches. Through their structure, dense *P. oceanica* meadows attenuate wave energy in shallow depths (Manca et al., 2012). For example, Infantes et al. (2012) recorded a reduction of 50% of wave height in places where *P. oceanica* meadows had a density of around 600 shoots m^{-2}. Moreover, by decreasing the wave energy reaching the shore, *P. oceanica* meadows limit the height of waves crashing on a beach (Manca et al., 2012). *P. oceanica* meadows therefore provide natural protection for beaches against coastal erosion (Gacia and Duarte, 2001; Vacchi et al., 2017).

Through exposure to water movement and its seasonal physiological characteristics, *P. oceanica* meadows export part of their primary production to the shore (Boudouresque et al., 2006); this process occurs mainly during autumn and winter storms. The exported material, which comprises leaves, roots and rhizomes, accumulate on sandy beaches and form 'banquettes' (Fig. 7) – a pile of *P. oceanica* litter that can reach a height of several meters (Boudouresque et al., 2015). Banquettes are eroded at their bases by waves, resulting in the formation of an arched overhang (Mateo et al., 2003), while they limit sediment loss from a beach, hence reducing coastal erosion (Chessa et al., 2000; De Falco et al., 2008). Banquettes act as temporary sinks of biogenic elements, given that *P. oceanica* meadows are able to accumulate 50% of their biomass, 71% of their carbon, 27% of their nitrogen and 9% of their phosphorous (Mateo et al., 2003). Slow degradation of beach banquettes releases nutrients that are then available for terrestrial organisms (Guala et al., 2006). Such nutrient input has been assessed for the upper beach and fore dune vegetation (Fig. 7), and found to enrich terrestrial plant tissues by a factor of 1.5 for nitrogen and up to a factor of 2 for phosphorous (Cardona and García, 2008; Del Vecchio et al., 2013). Such organic material is, however, of no benefit as food for beach macroinvertebrates, such as the sand hopper *Talitrus saltator* Montagu, as these do not feed on *P. oceanica* wrack. However, the physical structure of banquettes provides them with a shelter against predation and other adverse environmental factors (Colombini et al., 2009).

As already mentioned above, *P. oceanica* seascapes interact both with shallower and deeper marine ecosystems through export of detritus (Fig. 7). This output of *P. oceanica* ecosystems is called "necromass", *i.e.* exported primary producers, leaves, broken rhizomes and roots as well as drift macrophytes (Boudouresque et al., 2015). The amount of necromass exported ranges from 10 to 55% (Boudouresque et al., 2015), while this percentage varies strongly between one place and another; for instance 51–68% recorded from Marseille (France) and 37–49% from Ischia (Italy) (Pergent et al., 1997; Pergent et al., 1994). Differences in the amount of exported necromass probably result from differences in water movement intensity during autumn and winter storms (Remy, 2016), as well as from *P. oceanica* seascape structure, with patchy meadows accumulating less detritus than continuous ones (Ricart et al., 2015).

Although the primary production exported from *P. oceanica* meadows is well studied, data on its destination and use in other marine seascapes are scarce. Presumably, the first marine habitats taking advantage of this input are those located adjacent the seagrass meadows,
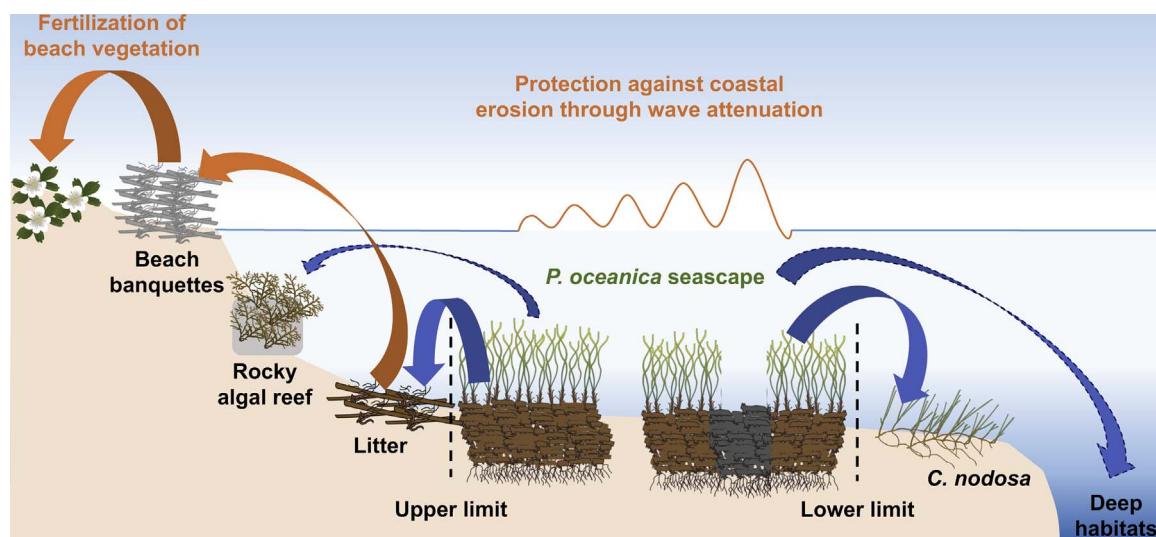

Fig. 7. Schematic diagram showing connectivity of a *P. oceanica* seascape with terrestrial ecosystems and other marine habitats. Orange arrows: terrestrial connection; blue arrows: marine connection. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

for example bare sediment habitat, algal forests and meadows formed by other seagrass meadows (Fig. 7). Thus, *P. oceanica* outputs are a carbon source for sand-dwelling species living close to the meadow, while this has not been established for more distant ecosystems (Cardona et al., 2007). More than a simple food source, *P. oceanica* necromass, in the form of submerged 'litter' on the seabed, creates a temporary mobile habitat and provides a structured shelter for a whole unique set of detritivore invertebrates (Dimech et al., 2006; Mascart et al., 2015; Remy, 2016).

In the case of marine ecosystems located at a large distance from *P. oceanica* meadows, few studies have addressed the quantity and potential use of export of necromass from the seagrass ecosystem. It is assumed that most of this resource is consumed by the sea urchin *Paracentrotus lividus* present on sublittoral rocky bottoms and reefs (Verlaque and Nedelec, 1983) as well as serving as a source of organic matter for algal habitat on hard bottoms (Cardona et al., 2007) and marine caves (Picard, 1965). However, such export is probably less than expected given the lower efficiency of *P. oceanica* energy transfer (2–10 times lower) to higher trophic levels when compared to other Mediterranean seagrasses such as *Cymodocea nodosa* (Ucria) Ascherson and *Zostera noltii* Hornemann (Danovaro et al., 2002). Organic material exported by *P. oceanica* is also expected to reach deep water habitats to depths of around 600 m (Gobert, personal observation; Fig. 7) (Wolff, 1976).

4. Information on *P. oceanica* seascapes for management purposes

Although a large effort has been made to understand aspects of seascape ecology over the last fifteen years, there are still limitations with regard to both data acquisition and mining and treatment when compared with terrestrial landscape studies. Moreover, there remain difficulties concerning the development of tools for managers and stakeholders who, ultimately, are the eventual users of information on seagrass seascape ecology. These assertions are particularly true for *Posidonia oceanica* seascapes and their management within the framework of European directives such as the Water Framework Directive (WFD) and the Marine Strategy Framework Directive (MSFD).

4.1. Data acquisition and treatment

One of the most widespread tools used in landscape ecology to collect information at large spatial scales is habitat mapping. Currently, the most popular techniques used in habitat mapping use Geographical Information Systems (GIS). Improvement of data acquisition techniques in recent years has enabled the production of extensive marine habitat maps (Leriche et al., 2004; Noël et al., 2012), which have become as important as the mapping techniques used in terrestrial ecological studies and the information generated thereof. Side scan sonar images (or sonograms), have a high resolution when used in mapping surveys of the marine environment, and can give a clear visual indication of seascapes formed by *P. oceanica* meadows. This information can be used to highlight the impacts of human activities on seagrass beds (Abadie et al., 2015; Leriche et al., 2006; Pasqualini et al., 1999). However, since side scan sonar requires use of a towed device, it cannot be operated at depths shallower than 10 m (Augris and Clabaut, 2001), thus limiting data acquisition on extensive shallow coastal areas that support seagrass meadows. To counteract this limitation, side scan sonar images are used in conjunction with aerial and satellite imagery techniques that allow accurate determination of the distribution of seagrass meadows and patches of the habitat.

As already stated, *P. oceanica* seascapes present a heterogeneous vertical structure whose formation in influenced by seafloor features and dynamics of the seagrass matte. A tri-dimensional approach is required to study the structural and functional features of the habitat. Mapping techniques currently used in landscape and seascape ecology utilize the two-dimensional (2D) aspect because this is simpler to generate and requires less data than ones having a three-dimensional (3D) aspect. The creation of 3D maps is, however, very widespread in terrestrial environmental studies, especially in programs that have an educational or informative aim (Niedomysl et al., 2013; Schobesberger and Patterson, 2008). Besides the advantages and inconvenience of visual interpretations (Popelka and Brychtova, 2013), 3D maps provide different results compared to the 2D ones according to the topography of the site studied. Moreover, some metrics traditionally used with 2D maps remain applicable to 3D analyses but, still, it is essential to create new ones (Parrott et al., 2008; Wu et al., 2012).

In the marine environment, particularly in the case of seagrass meadows, site topography has a strong influence on the species' spatial distribution in different habitats (Robinson et al., 2011). Within the context of gathering information for use in conservation measures, use of 3D mapping surveys could help managers understand the importance and functioning of marine habitats. In the case of *P. oceanica* meadows, it is clearly established that water depth (Elkalay et al., 2003) and seafloor features (Di Carlo et al., 2005) play an essential role in influencing seagrass meadow dynamics. Thus, beyond the purely visual aspect, use of 3D maps in a seascape study should provide a more realistic view of patch arrangement and function. For instance, it seems logical that a *P. oceanica* vertical edge having a height of 2 m which appears flat on classical maps (2D) would constitute a real obstacle for the movement of several benthic organisms. Moreover, it is not only the aboveground structure that should be considered in a 3D analysis, but also the belowground one; namely the root-sediment matrix that also influences a *P. oceanica* seascape (Abadie et al., 2016).

The number of *P. oceanica* habitat mapping studies, as well as works assessing their functional role, have increased over the last two decades (Boström et al., 2011; Telesca et al., 2015). It would thus be tempting to extrapolate functional features at a large spatial scale from the available maps to manage coastal habitats. However, several obstacles prevent such approach for marine habitats in general, including *P. oceanica* seascapes.

Although the number of available maps of *P. oceanica* habitat has increased, there are still problems concerning lack of data on their functioning, and on how to acquire the necessary information. While it would seem appropriate to study structural and functional processes at a small spatial scale (*i.e.* smaller than 1 km^2) using quadrats, discrete sampling techniques and transects (Pace et al., 2017), such techniques are less adequate for studies at the medium (1–10 km^2) and large (> 10 km^2) spatial scales. A first obstacle thus lies in the methods used for large spatial scale studies. Even if 62% of such studies have relied on mapping, 20% of them have been made using quadrats and discrete sampling techniques (Table 2). Evidently, new field methods need to be developed to assess the functional aspect of seagrass seascapes at large spatial scales; for example, automated fish and macroinvertebrate counting made using Remotely Operated Vehicles.

Furthermore, as described above, sampling effort has been focused on a small number of species that have contrasting mobility (Boström et al., 2006; Connolly and Hindell, 2006). Linking direct observations with maps requires addressing aspects of interest indicated by a numerical data, such as width of the edge effect and maximal propagation/dispersal distance of species between one patch and another (Boström et al., 2011; Olds et al., 2016). Unfortunately, even on

Table 2
Proportion (%) of sampling methods used in studies of *P. oceanica* that consider one or more spatial scales. SSS: Small Scale; MSS: medium scale; LSS: Large scale; Q-DS: Quadrat-Discrete Sampling; T: Transect; SP: Small Patch; LP: Large Patch; M: Mapping.

	Q-DS	T	SP	LP	M
SSS	39	6	24	6	24
MSS	12	24	0	4	60
LSS	20	13	4	0	62

obtaining such data, the information acquired using the available methods may not reflect the true situation due to the complexity of species-rich ecosystems such as *P. oceanica* seascapes (Duffy et al., 2007; Green and Sadedin, 2005). Such an obstacle can be overcome by using new approaches to data management and treatment based on meta-analysis of available data, which help answer a specific question. However, such an approach first requires homogenization of databases as well as total and free access to data resources; this field has been recently referred to as 'big science' (Hampton et al., 2013). When these conditions are met, it is possible to proceed with analysis of complex biological systems, such as *P. oceanica* seascapes, through data mining (Hochachka et al., 2007) and artificial intelligence (Rykiel, 1989). From fundamental approaches, new simplified tools and land/seascape assessment procedures aimed for use by coastal managers have already emerged; these indicate the limitations of previous techniques.

4.2. New analysis tools for management purposes

Over the last few decades, several indices have been developed for use in landscape ecology to quantify the spatial features of terrestrial habitats (McGarigal et al., 2014; Schumaker, 1996). These metrics have been transferred to marine studies and are currently widely used for management of seagrass seascapes, including ones formed by *P. oceanica* (Chefaoui, 2014; Montefalcone et al., 2013; Sleeman et al., 2005). However, recent studies concerning terrestrial ecosystem conservation have highlighted their limits (Kupfer, 2012; Šímová and Gdulová, 2012) the same observation being made for seascapes (Manderson, 2016). Specifically, information on the relationship between some specific metrics and ecological processes (Fig. 8) are sometimes doubtful (Li and Wu, 2004). Consequently, landscape indices should not be used alone when studying *P. oceanica* seascapes, while the outcomes should not be considered as the ultimate tool for management decisions but rather require coupling with other landscape procedures and

interpreted using knowledge of ecological processes (Fig. 8). The limitations of landscape indices also highlight the need for new practical ways to provide information on seascapes to stakeholders.

Traditionally studied as a patch mosaic, landscapes can also be described within the context of a more functional angle by using an approach called the 'landscape graph' (Fig. 9) (Kupfer, 2012). Applying the mathematical theory underlying landscape graphs to landscape ecology results in nodes (2D patches) connected by links (from the perimeter or the centre) inside a matrix (Fall et al., 2007). Links can be drawn as Euclidean distances (straight lines), and as lowest cost (for instance according to relief or habitats), or else weighted using ecological factors. Different graph types can be built and modelled, for example, making links between all nodes or only making nodes close to another (Galpern et al., 2011). The generation of landscape graphs requires the use of new metrics to study landscape characteristics. This type of model is, however, limited as it only takes into account the landscape connectivity characteristics but not habitat quality (Moilanen, 2011).

The use of landscape graphs for the study of *P. oceanica* seascapes will be an important breakthrough in understanding the influence of meadow structure on the occurrence and distribution of associated biota. Within the context of conservation and management, graphs will help us gain insight of important aspects (Galpern et al., 2011) such as: (1) nodes are connected in a seascape; (2) which patch types are important for connectivity; (3) which patches are important for connectivity; (4) how connectivity differs between graphs; (5) the threshold of aggregation within a landscape. The knowledge gained will be very useful for managers involved in the conservation and management of seagrass habitat. The Landscape Graphs Model thus allows better communication of knowledge on important ecological aspects with decision-makers (Bergsten, 2013).
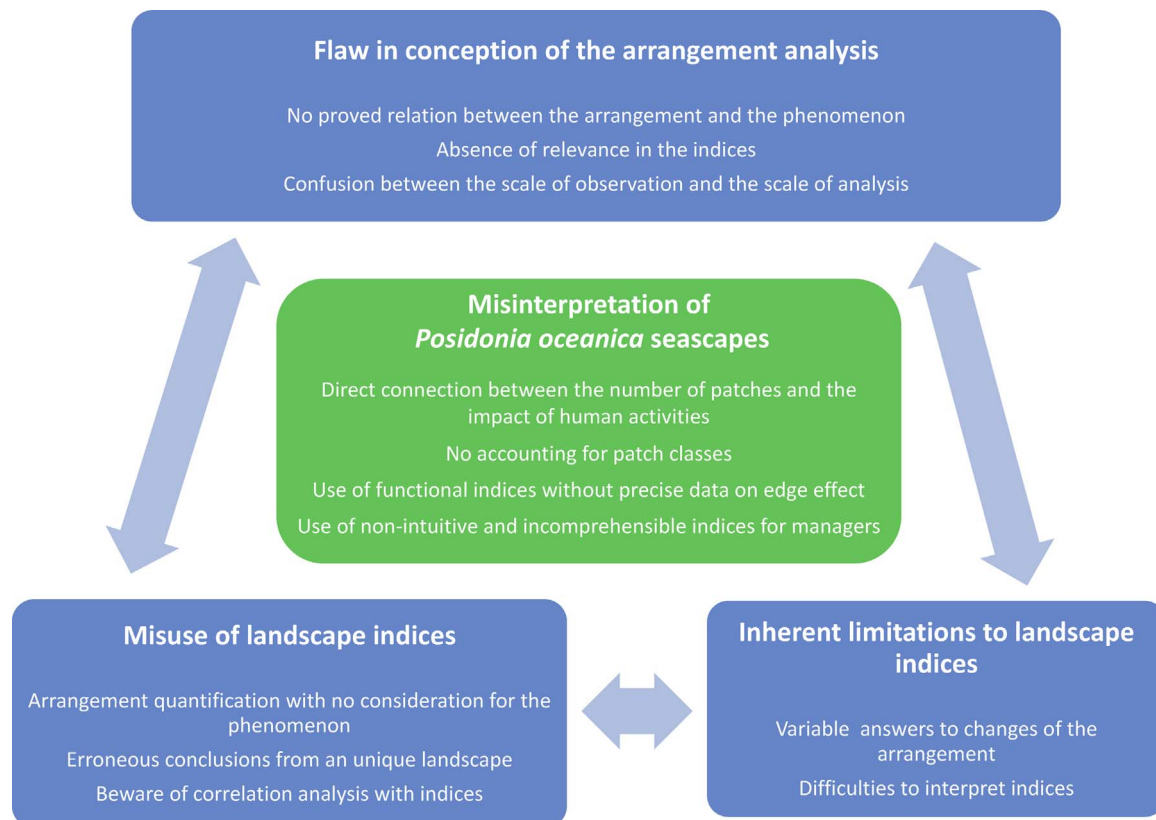
Flaw in conception of the arrangement analysis

No proved relation between the arrangement and the phenomenon
Absence of relevance in the indices
Confusion between the scale of observation and the scale of analysis

Misinterpretation of *Posidonia oceanica* seascapes

Direct connection between the number of patches and the impact of human activities

No accounting for patch classes

Use of functional indices without precise data on edge effect

Use of non-intuitive and incomprehensible indices for managers

Misuse of landscape indices

Arrangement quantification with no consideration for the phenomenon
Erroneous conclusions from an unique landscape
Beware of correlation analysis with indices

Inherent limitations to landscape indices

Variable answers to changes of the arrangement
Difficulties to interpret indices

Fig. 8. Issues encountered when using indices in landscape ecology (blue) and their impact on the study of *P. oceanica* seascapes (green) [modified from Li and Wu (2004)]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
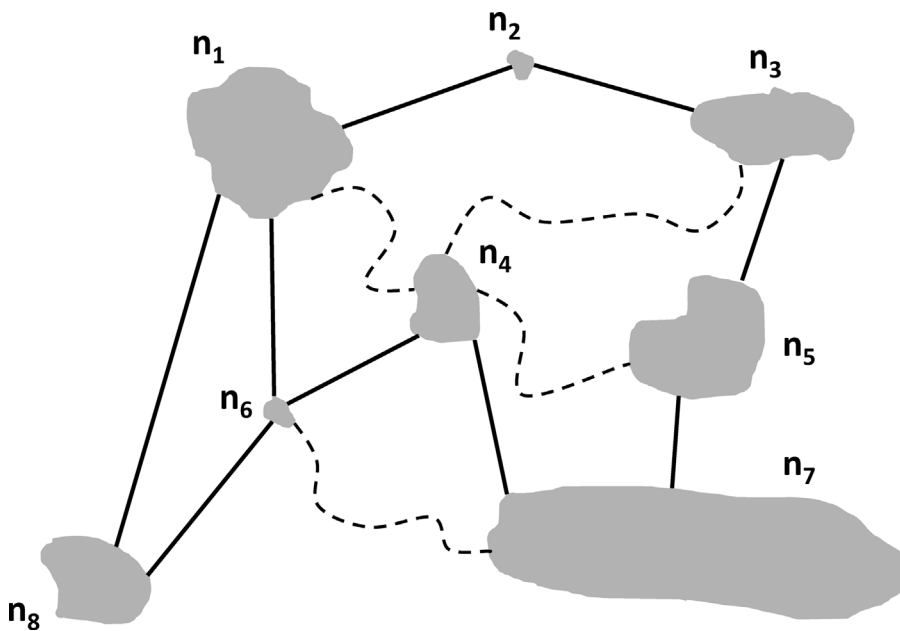
5. Conclusion

Amongst the seascapes formed by different seagrasses, *P. oceanica* meadows are the most studied due to their peculiar and complex three-dimensional structure and the large number of species they support. Over the last 15 years, there has been a large effort to study their large-scale structural features and interactions with fauna and flora, which has resulted in important data being available for use in management of the habitat. However, much work remains to be done at the level of data processing as well as to enhance transfer of information on seagrass seascape ecology to managers and stakeholders. With this in mind, efforts to automatize the treatment of spatial and environmental data must be emphasized. New approaches and simplified procedures are currently available for landscape ecological studies but these cannot always be applied to seascape ecology due to lack of data. More specifically, there is gap in fundamental knowledge concerning the spatial distribution of key species (such as *P. lividus* and *S. salpa*) linked with the structure of seagrass seascapes. Hence, there is need for ecological studies aimed at gathering the necessary information as well as to develop new tools and procedures including ones aimed at studying *P. oceanica* seascapes. In the same way, critical environmental issues such as climate change and pollution may be studied including seascape aspects and thus provide a spatial and evolutionary point of view to coastal managers.

In a wider viewpoint, landscape ecology has become a bridge between scientists and stakeholders, thus allowing fundamental researches to be applied for conservation and management. When, dealing with seagrasses, especially with *P. oceanica*, seascape ecology seems promising for use in policies and protection enforcement, particularly given the increasing public interest on marine Magnoliophytes and the habitats they contribute to.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolind.2017.12.029.

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