Marine space ecology and seagrasses. Does patch type matter in *Posidonia oceanica* seascapes?

Arnaud Abadie[a,b,c], Sylvie Gobert[c], Marina Bonacorsi[b], Pierre Lejeune[a], Gérard Pergent[b], Christine Pergent-Martini[b]

[a] *Station de Recherches Sous-marines et Océanographiques (STARESO), Pointe Revellata, BP 33,20260 Calvi, France* [b] *EqEL - FRES 3041, UMR CNRS SPE6134, University of Corsica, Campus Crimaldi, BP52,20250 Corte, France* [c] *Laboratory of Oceanology - MARE Centre - University of LIEGE - B6C- 4000 LIEGE - Sart Tilman, Belgium*

ABSTRACT

The use of landscape tools in the study of seagrass meadows (seascapes) begins to be widely spread but still require the establishment of several basis, i.e. a patch type classification based on numerical characteristics. Thanks to the complex seascapes created by the *Posidonia oceanica* meadows, they appear to be suitable for a study at a patch type level (class), which bring a new insight of their arrangement at the whole seascape scale. By interpreting side scan sonar images from the Corsican coast (France) through a GIS software, it was possible to describe 11 types of patches and to evaluate their natural or anthropogenic origin. Comparison of different landscape metrics and wave exposure (Relative wave Exposure Index, REI) at the seascape and the patch level showed that the particularity of P. *oceanica* seascapes are mainly characterized by certain types of patches often of anthropogenic origin. Furthermore the REI seems not to be a relevant index for a study at a class scale. A bathymetrical succession of natural patches was outlined from the lower to the upper limit of the meadow, with a long-term dynamic opposed to a shorter one concerning anthropogenic patches. In order to assess the origin (natural or induced by human activities) of the patches in *P. oceanica* meadows, as well as in any other seagrass, a Patchiness Source Index (PaSI), ranging from 0 to 1, was defined.

Keywords: Seagrass Seascape Patchiness Side scan sonar Human impact

1. Introduction

Over the last three decades the interest in landscape ecology has grown and spread from land to marine ecosystems (Li and Mander, 2009; Sousa, 1984). A seascape can be defined as the varying arrangements of biotic structures with the resulting mosaic of marine habitat patches (Robbins and Bell, 1994). Thus, the study of their function and heterogeneity, including fragmentation and patchiness, should be called the Marine Space Ecology (Li and Mander, 2009). Fragmentation refers to a dynamic process which cannot be studied given a single temporal set of data (Boström et al., 2011). This term is often used in an erroneous way in place of patchiness which refers to a static state of a landscape.

The Mediterranean meadows of the seagrass *Posidonia oceanica* (Linnaeus) Delile play an important ecological and economic role e.g., fish nursery, carbon sink, protection from coastal erosion (Boudouresque et al., 2012; Costanza et al., 1997; Ruiz et al., 2009; Vassallo et al., 2013). Generally dense and continuous in the coastal zone from the surface to 45 m depth (Molinier and Picard, 1952), they are nevertheless subject to fragmentation due to natural phenomena and human activities (e.g. coastal development, pollution, anchoring) (Ardizzone et al., 2006; Boudouresque et al., 2009). In order to assess the role played by the heterogeneity of seagrass meadows, a landscape approach should be used (Bell and Hicks, 1991; Gobert et al., 2014; Robbins and Bell, 1994).

Heterogeneity in the physical structure of a seagrass meadow plays a major role in its functioning (e.g. juvenile survival, species-lined settlement, colonization, predator movements) thanks to the size and the shape of the patches (Bell et al., 2001; Borg et al., 2006; Boström et al., 2006; Connolly and Hindell, 2006; Micheli and Peterson, 1999). The habitats created by a natural fragmentation are essential for several key species (Prado et al., 2009).

Between 1950 and 1990 many types of P. *oceanica* seascapes have been described (Boudouresque et al., 2012,1990,1980a, 1985, 1980b; Clairefond and jeudy De Grissac, 1979; Molinier and Picard, 1952,1954; Pergent et al., 2007). These descriptions (Table A1) only refer to a visual aspect of the structures that forms P. *oceanica* and do not take into account those induced by human activities. Moreover, each of these structures was described by using scuba diving observations, large-scale tools with enough accuracy (e.g. side scan sonar) being not available at that time.

P. *oceanica* meadows show natural forms of heterogeneity in their structure under the shape of sandy patches as well as "bare mat" (or "dead matte") areas. The term "matte" (or "mat") was originally used by French Mediterranean fishermen to refer to the complex structure formed by P. *oceanica* rhizomes, roots and sediments (Molinier and Picard, 1952). Sandy patches seem to be generated by the water movement as well as depend of the slope and the substrate of seagrass beds (Blanc and Jeudy De Grissac, 1984). These gaps are traditionally named "intermattes", literally translated "space between the matte". The designation "inter-matte" has been used for every type of sandy or bare mat patches while there are no discontinuities in the mat in the case of the latter. For this reason we will use hereafter the designation "patch" to refer to any type of discontinuity in a meadow. Moreover, this term is the one commonly used in landscape ecology. Other endings corresponding to "patch elements of one habitat within a matrix of another" (Boström et al., 2006) can be applied to seagrass seascapes like "sand holes" (Ginsburg, 1956), "blowouts" (Patriquin, 1975), "spaces" (Sousa, 1984), "halos" (Fonseca and Bell, 1998), "gaps" (Bell et al., 1999) or "corridors" (Micheli and Peterson, 1999).

Bare mat areas can be natural or induced by human activities like the organic matter loads of fish farms (Pergent-Martini et al., 2006), trawling (Kiparissis et al, 2011; Pergent et al., 2013), explosives (Meinesz and Lefèvre, 1983), pollution (Pergent-Martini et al., 1995) or damages of boats anchoring (Montefalcone et al, 2006b). Several of these seascape parts of P. *oceanica* meadows are assumed as "dynamic" and appear to modify their shape and surface through time. Hereafter we define a *"Posidonia oceanica* seascape" as the set of the different habitats (i.e. types of patch) of natural and anthropogenic origin included in a meadow matrix.

In the present study we focused on the spatial relationships among distinct elements (patches, matrix), an approach that is still seldom used. The major advances and steps in the study of seagrass seascapes through time are summarized in Fig. A1. Due to the complexity (Boudouresque et al., 2012) and the various types of habitats (Borg et al., 2006) encompass by P. *oceanica* meadows it appears to be possible to study their seascapes characteristics at the class patch type level (class). All the patches mentioned above can be identified with the use of side scan sonar (Bonacorsi et al., 2013; Leriche et al, 2006; Pasqualini et al., 1999) and from the resulting mapping many landscape indices may be computed by using software programs (Bell et al., 2006; McGarigal et al., 2014; Sleeman et al, 2005). Thus we (1) described natural and anthropogenic patches in several P. *oceanica* meadows; (2) established a nomenclature of these structures based on their origin, shape and surface; (3) investigated the relation between various types of patches and the P. *oceanica* seascapes observed using landscape metrics and we attempt to link it with the local water movement (Murphey and Fonseca, 1995); (4) finally we explored the possibility of using patches in seagrass meadows to assess the source of patchiness of P. *oceanica* seascapes.

2. Material and methods

2.1. Sites and data acquisition

Data on P. *oceanica* meadows were acquired in Corsica (France) during the Cartham program in summer 2010 on the West coast, and CoralCorse program in summer 2013 on the East coast (Fig. 1). Sonograms were obtained using a side scan sonar Klein 3000® and the SonarPro® software. This device sends a high frequency acoustic signal (500 kHz) reflected by the sea floor and received by the ship. The intensity of the signal sent back allows the determination of the bottom nature. The data acquired were processed with the Caraibes 3.8® software program (georeferencing, optimization of the quality of sonograms). A mosaic of merged sonar images (resolution of 0.5 m) was developed.

From these georeferenced sonograms, five sites within continuous P. *oceanica* meadows and corresponding to as many types of P. *oceanica* seascapes as possible were selected along the coastline. Furthermore, one of the main selection criterion was the presence of possible traces of human impacts. Three sites were chosen on the East

coast (South of Macinaggio, the open sea in front of Biguglia and Urbinu lagoons) and two on the West coast (Calvi Bay and the Gulf of Ajaccio) (Fig. 1).

2.2. GIS processes

When clearly identified, the limits of sandy and bare mat patches in P. *oceanica* meadows were drawn in the GIS software. Their origin was estimated by looking for the presence of human activities in the neighborhood of the patches. Only patches detectable and recognizable with the sonar resolution are taken into account, that is to say those having an area greater than 1 m². Thanks to this resolution it is thus possible to take into account the smallest patches. The GIS files were finally transformed into rasters (GeoTIFF grid) and analyzed through the computer program FRAGSTATS version 4.2 to obtain landscape indices.

2.3. FRAGSTATS analysis

The FRAGSTATS software, first developed by McGarigal and Marks (1995), allows the calculation and the analysis of various seascapes metrics at three scales: the patch, the type of patch (class) and the entire seascape. In the present study only the patch class and the entire seacape are investigated. No metric was calculated at the patch level. The analysis was performed using an eight cells neighborhood rule coupled with no specific sampling strategy to consider the whole part of meadow selected. Following the recommendations of Sleeman et al. (2005), seven metrics were chosen for the analysis of the seascapes patchiness: the mean patch area (AREA), the mean radius of gyration (GYRATE_MN), the area-weighted radius of gyration (GYRATE_AM), the coefficient of variation of the Euclidean nearest-neighbor distance (ENN_CV), the area-weighted perimeter-area ratio (PARA_AM), the landscape division index (DIVISION) and the number of patches (NP) (Table A2). The same metrics were chosen for the patch type (class). At the seascape level the patch density (PD) was also calculated.

2.4. REI calculation

In an effort to link the erosive structures observed and the landscape metrics measured with the local water movement, we investigated the exposure of the sites to different wind conditions by using the Relative wave Exposure Index (REI) developed by Keddy (1982) and modified by Murphey and Fonseca (1995):

$$REI = \sum_{i=1}^{8} (V_i \times P_i \times F_i)$$

where i = 1 to 8 corresponding to cardinal points in 45° increments (N=1, NE = 2, etc.), V=mean monthly mean wind speed (ms^{-1}), P= rate of wind direction occurrence and F= effective fetch (km) or the distance from the site to the land computed through the 8 compass headings. Daily wind direction and speed were obtained from forecast stations at a distance of 4,13, 6, 35 and 12 km respectively for the sites of Calvi, Macinaggio, Biguglia, Urbinu, and Ajaccio. Due to the availability of meteorological data for all sites only for the year 2011, V and P were computed for this single year. Fetch was calculated using the method of Fonseca and Bell (1998) by using ArcGIS®.

2.5. Statistical analysis

Two principal component analysis (PCA), one for each scale of study (class and seascape), were performed using R version 3 software. The landscapes indices and the REI values were computed to assess the difference of seascape characterization according to the spatial degree of consideration. The variable loadings were checked to make sure that the indices chosen were significantly informative about the P. *oceanica* seascape structure at both landscape and class level.

2.6. Patchiness Source Index (PaSI) calculation

In order to assess the main origin (natural or anthropogenic) of the patchiness observe in P. *oceanica* seascapes, we defined a Patchiness Source Index (PaSI) for a given area by computing surfaces of the different structures identified. The PaSI is based on the model of the Conservation Index (CI) developed by Moreno et al. (2001):

$$PaSI = S_{NP}/(S_{NP} + S_{AP})$$

where S_{NP} = percentage of the surface covered by the different types of natural patches (m^2) and S_{AP} = percentage of the surface covered by different types of anthropogenic patches (m^2). The PaSI ranges from 0 to 1 and has no unit. A value tending to 0 reflects a meadow patchiness mainly due to human activities. On the other hand, a value near 1 should reflect a natural patchiness. PaSI values are classified using five categories and a color code (Table 1).

Fig. 1. location along the Corsican coast of the sites considered in this study.
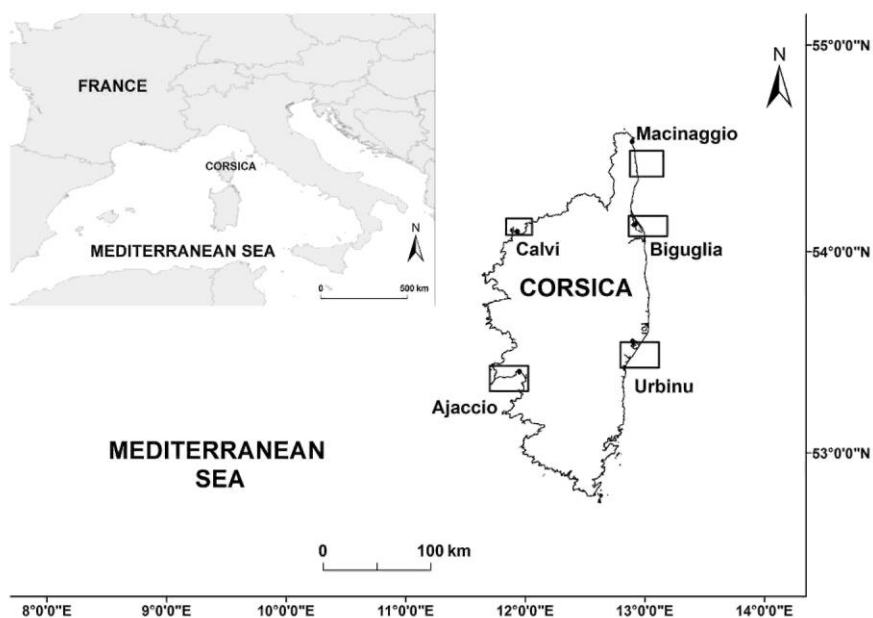
Table 1 : Color code corresponding to the different values of the Patchiness Source Index (PaSI).

PaSI Value	Description	Color
0.801 -1	High natural influence on the meadow patchiness	Blue
0.601 - 0.800	Major natural influence on the meadow patchiness	Green
0.401 - 0.600	Moderate anthropogenic influence on the meadow patchiness	Yellow
0.201 - 0.400	Major anthropogenic influence on the meadow patchiness	Orange
0 - 0.200	High anthropogenic influence on the meadow patchiness	Red

3. Results

3.1. Patches characteristics

The meadow of the South of Macinaggio shows bomb craters and natural sandy patches (Fig. 2a). In front of Biguglia lagoon the meadow is covered by trawling tracks, large marks made by tankers anchors and chains as well as several sandy natural patches (Fig. 2b). Many sandy corridors and ovoid patches of various sizes are observed in front of Urbinu lagoon (Fig. 2c). The meadow chosen in Calvi Bay shows various types of patches like anchoring tracks, fish farm impact, bare mat patches and other natural structures (Fig. 2d). Finally, a high patchiness near the fish farm is observed on the meadow selected in the Gulf of Ajaccio (Fig. 2e).

The analysis of the sonograms allowed the detection of 11 different types of patches in the meadows (Table 2). Five were likely to be of natural origins whereas five were induced by human activities. The origin of bare mat patches was hard or even impossible to be determined with the sonar images alone.

The shape of natural patches showed a bathymetric zonation. Thus, sand corridors (SC) were observed from 10 m to 20 m depth, small sand patches (SSP) at the same depth, large sand patches (LSP) and colonized patches (CP) from 15 to 25 m while ovoid patches (OP) were encountered between 15 m and the lower limit of the meadow (Table 2). This particular zonation was mainly observed on the sonograms of Biguglia, Urbinu and Calvi. All the natural patches presented various sizes, their surface ranging from 1 m^2 to 25,544 m^2 (Fig. 3).

The natural and anthropogenic bare mat patches presented various sizes and shapes so their sonar images can be very similar (Table 2). Due to their size and shape that greatly depended of the human activities involved in their creation, the anthropogenic patches were quiet easy to identify. The narrowest ones were the trawling tracks and the anchoring tracks (from 0.5 m to 4.0 m large) which were also the longest i.e. up to 1800 m for the trawling tracks and 230 m long for the anchoring tracks (Table 2). Patches generated by the anchoring of cruise ships and/or tankers reached a surface of 1254 m^2 with a characteristic "funnel" shape. The biggest surfaces were observed at the level of the bomb impacts (57,686 m^2) and of the patches generated by the fish farms (more than 100,000 m^2 for a single patch) (Fig. 3). Generally speaking, bare mats cover a small part of the P. *oceanica* seascapes studied, that is to say a mean coverage of 1.4% (SE ± 1.7%).

3.2. Seascapes features

At a seascape level, the different sites showed great variations in their landscape indices and REI values leading to various P. *oceanica* seascapes (Table 3). The number of patches (NP), ranges from 66 in the South of Macinaggio to 1473 in Urbinu. Concerning the patch density (PD) the site of Biguglia looked as the patchiest (291.5 patches m^{-2}) whereas the South of Macinaggio was the lesser one (12.5 patches m^{-2}) (Table 3). The mean size of patches (AREA_MN) reached its highest value in the South of Macinaggio (80,160 m^2) and its lowest in Calvi (4186 m^2). The mean distance of patches gravity center from their border (GYRATE_MN) showed high variations too, from 33.34 m in the South of Macinaggio to 3.98 in Urbinu. By taking into account their area with the area-weighted radius of gyration (GYRATE_AM), its values greatly increased, from 1056.50 m in the South of Macinaggio to 510 in Calvi. It means that in a landscape-centric perspective the necessary distance to reach the edge of a patch will grow longer respectively for Calvi, Urbinu, Ajaccio, Biguglia and the South of Macinaggio. A high coefficient of variation (ENN_CV) of the mean distance between each patch for each site was observed, describing a high spatial heterogeneity in patch arrangements for all sites (Table 3). The Landscape Division Index (DIVISION) values reflect low divided meadows for the sites of Calvi, the South of Macinaggio and Biguglia whereas the sites of Ajaccio and Urbinu are more fractionated. The exposition of the sites to wave action illustrated by the REI showed contrasted values that discriminate the sites in three groups. Ajaccio was relatively not exposed (253) whereas Calvi (1855) and Urbinu (3239) were well exposed to wave action, when Biguglia (11,038) and the South of Macinaggio (15,161) are very exposed (Table 3). Using the PaSI on the sites studied, it ranked 0.412 for Ajaccio, 0.350 for Calvi, 0.547 for the South of Macinaggio, 0.591 for Biguglia and 1 for Urbinu, revealing contrasted sources of patchiness (Table 3).

3.3. Seascape versus class scale

The analysis through PCA of the metrics at the scale of the landscape and the patch type presented contrasted results. The five sites appeared to be well discriminated (Fig. 4) but these differences are mainly due to the landscape characteristics of a small number of patch type (Fig. 5). Thus this phenomena was partly driven by the small sand patches and the trawling tracks in Biguglia (SSP_BIG and TT_BIG), the anchoring patch in Calvi (AP_CAL), the fish farm patches and the anchoring tracks in Ajaccio (FFP_AJA and AT_AJA), the bomb impact in the South of Macinaggio (BLMAC) and the small sand patches in Urbinu (SSPJJRB) (Fig. 5). The large sand patches of Urbinu, South Macinaggio and Biguglia (respectively LSP.urb, LSP_MAC and LSP_BIG) form a group discriminated from the other patches because of their large surface (AREA_MN) and their

elongated shape (GYRATE.MN) (Fig. 5).

At the landscape scale the cumulative percentage of variance was almost 90% for the two axes. The variable loadings obtained from the PCA of the landscape metrics were high (≥ 0.3 or ≤ -0.3), except for the division index (DIVISION). This result indicates that the metrics selected were relevant to describe the patchiness of the landscape (Table 4). A different assessment was made concerning the variable loadings from the class level analysis. The two axis cumulated only 63% of the percentage of variance and the REI appears not to be relevant for a study at a patch type scale (Table 4).

Fig. 2. Examples of sonar interpretation of patches inside P. *oceanica* meadows for each site considered (a) South Macinaggio, (b) Biguglia, (c) Urbinu, (d) Calvi and (e) Ajaccio.
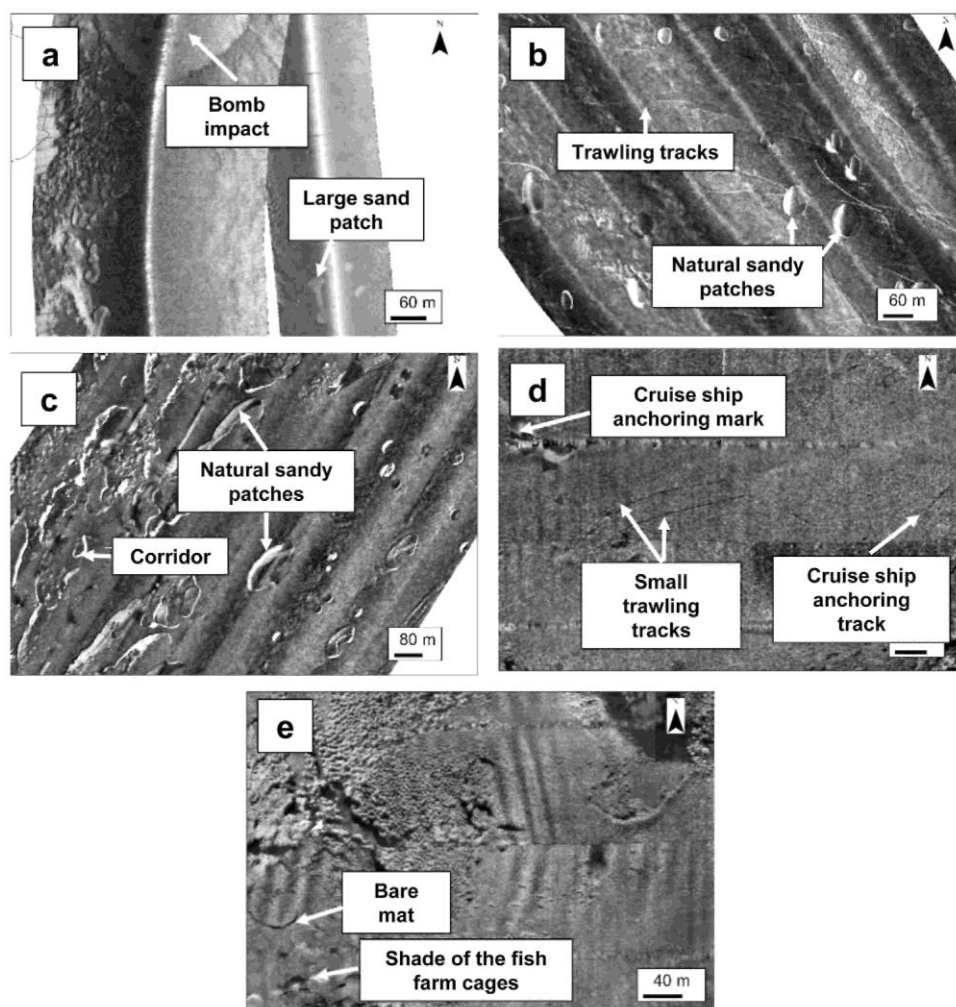
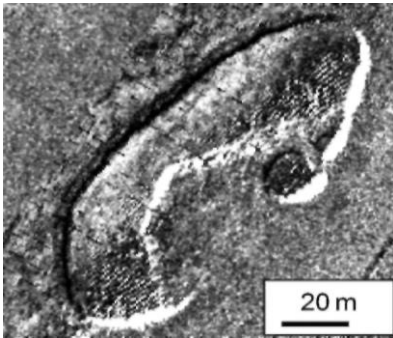**Table 2: Description of the different types of patches identified inside *Posidonia oceanica* meadows during this study.**
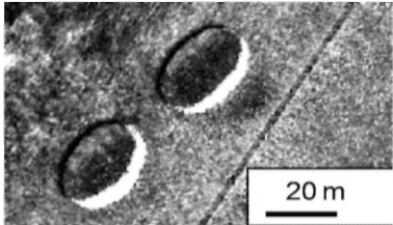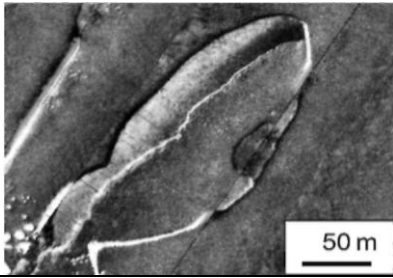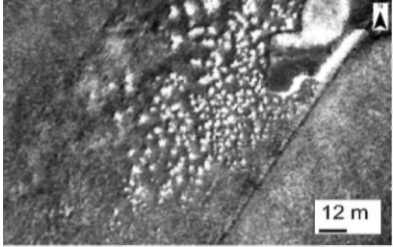
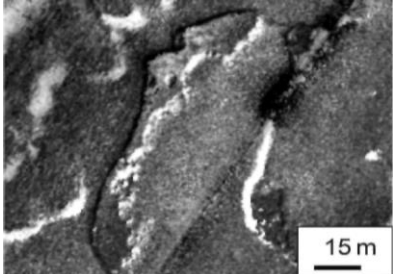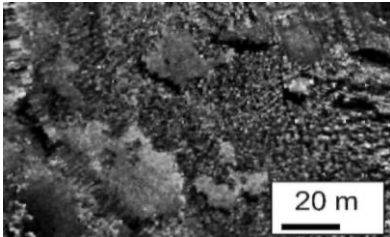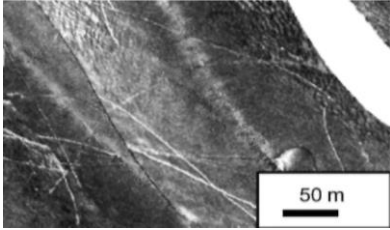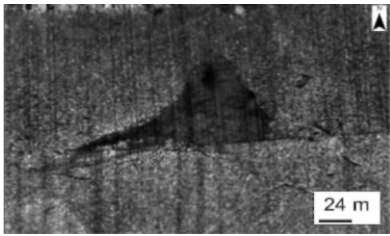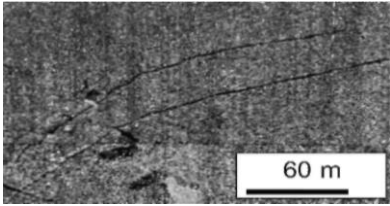| Sonogram	Designation	Description
	Ovoid patch (OP)	Ovoid shape with a length ranging from 20 to 60 m and a width from 15 to 30 m. Parallel to the coast. Observed from the lower limit of the meadow to 20 m deep. Most probably generated by the water movement
	Colonized patch (CP)	Ovoid shape with a triangle-like part recolonized by the meadow with a length ranging from 20 to 170 and a width from 15 to 65 m. Parallel to the coast. Observed from 15 to 25 m deep. Most probably generated by the water movement
	Large sand patch (LSP)	Banana shape with a length ranging from 70 to 500 m and a width from 30 to 50 m. Parallel to the coast. Observed from 20 to 15 m deep. Most probably generated by the water movement
	Small sand patch (SSP)	Small round craters with a width ranging from 1.5 to 6 m) that can link themselves and form narrow corridors. Mainly observed near larger patches like large sand patches or sand corridors from 20 to 10 m deep. Most probably generated by the water movement
	Sand corridor (SC)	Channel shape with a length ranging from 10 to 350 m and a width from 2 to 20 m. Parallel to the coast. Observed from 20 to 10 m deep. Most probably generated by the water movement

Table 2 *(Continued)*

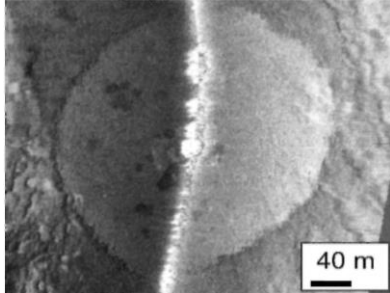| Sonogram	Designation	Description
	Bare mat (BM)	Mainly observed nearby the lower limit of the meadow but also frequently observed at lower depths. Patches of bare mat have irregular shapes and sizes. Certainly generated by winter storms and also by human activities. Possible confusion between the natural and the anthropogenic origins
	Trawling tracks (TT)	Long (100 m-1 km) and narrow (2-4 m) corridors generated by trawling in the meadow. Observed from 2 m to the lower limit of the meadows
	Anchoring patch (AP)	Funnel shape with a length ranging from 60 to 120 m. Parallel to the coast line certainly due to the main wind orientation. Observed from 20 to more than 30 m deep. Generated by the anchoring of cruise ships.
	Anchoring tracks (AT)	Corridors similar to trawling tracks but shorter (less than 250 m) and narrower (less than 2 m). Generated by both cruise ships and smaller leisure boats. Observed from 10 m to 35 m.
	Bomb impact (BI)	Circular patch generated by the impact of bombs mainly during the World War 2 or more recently by mines and explosive fishing. Their diameter ranges from several decameter to 250 m. Observed at all depths in the meadows
	Fish farm patch (FFP)	Bare mat patches nearby a fish farm generated by the shadow of the cages and the increase of the organic matter load. The acoustic image of the cages is visible. The extent of the patches varies according to the number of cages and their size. Generally it occurs at a depth ranging from 15 to 25 m

Fig. 3. Box plot representation of the surface areas of patches observed on all sites according to their type. The area is expressed through a logarithm scale. Black bars represent minimum and maximum patch areas. OP: ovoid patch; CP: colonized patch; LSP: large sand patch; SSP: small sand patch; SC: sand corridor; TT: trawling tracks; AP: anchoring patch; AT: anchoring tracks; BI: bomb impact; FFP: fish farm patch; BM: bare mat.
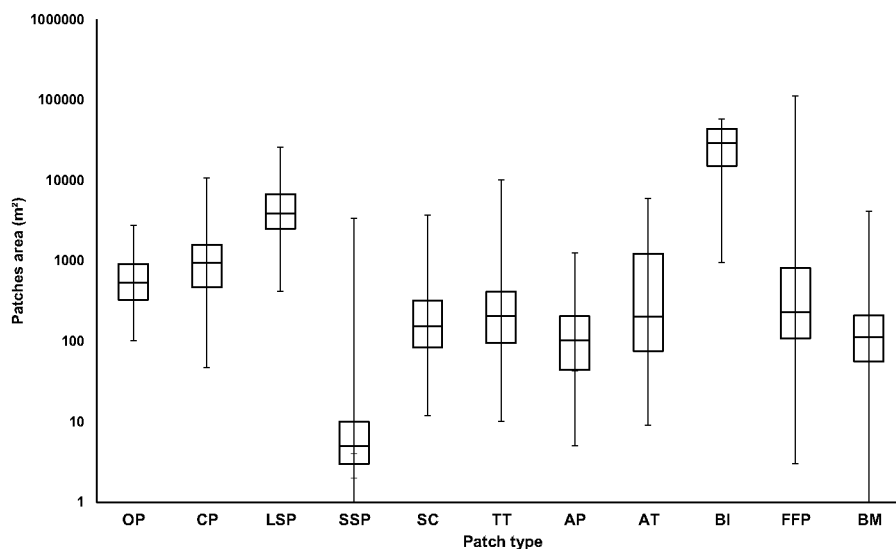

Table 3: Surface of the area and the *Posidonia oceanica* meadows, landscape indices, REI and PaSI values for the five sites studied.

Site	Metric scale	Ajaccio	Calvi	South Macinaggio	Biguglia	Urbinu
Surface of the area studied (km^2)	Seascape	2.451	1.858	3.583	4.423	2.129
Total meadow surface (km^2)	Seascape	2.201	1.765	3.394	4.167	1.849
Number of patches (NP)	Class and seascape	98	444	66	1290	1473
Mean patch area (AREA_MN) (m^2)	Class and seascape	24995	4186	80160	5875	13744
Patch density (PD) (patches.km^{-2})	Seascape	40.0	238.9	12.5	291.5	72.8
Mean radius of gyration (GYRATE_MN) (m)	Class and seascape	18.73	9.22	33.34	8.27	3.98
Area-weighted radius of gyration (GYRATE_AM) (m)	Class and seascape	663.43	510.15	1056.50	871.99	522.05
Coefficient of variation of the Euclidean nearest-neighbor distance (ENN_CV) (%)	Class and seascape	203.35	213.37	253.24	383.51	291.19
Area-weighted perimeter-area ratio (PARA_AM)	Class and seascape	180	578	108	809	470
Landscape Division Index (DIVISION)	Class and seascape	0.185	0.0978	0.1019	0.1222	0.2524
REI	Class and seascape	253	1855	15161	11038	3239
PaSI	Seascape	0.412	0.350	0.547	0.591	1.000

4. Discussion

4.1. From natural to anthropogenic Posidonia oceanica *seascapes*

This paper used side scan sonar images and cartographies of seagrass meadows in order to describe and establish a new nomenclature for P. *oceanica* patches and to perform an analysis of their characteristics at the large spatial scale of the seascape.

The first identifications and classifications of P. *oceanica* meadows were based on the observation of isolated patches at a small scale (Boudouresque and Meinesz, 1982; Molinier and Picard, 1952).This fact can be explained by the use of scuba diving prospections. Furthermore, anthropogenic patches were not considered as a component of the P. *oceanica* seascapes, only natural assemblages being described. Thus, the patches generated by human activities were studied independently. Our study demonstrated that nowadays certain P. *oceanica* seascapes are mainly characterized by some types of patches that can be of anthropogenic origin. That is why we advise to use a new nomenclature that define precisely each type of patch. The next step was the study of their relation to assess the P. *oceanica* seascapes structure. The patches attributes allow to infer on their possible origin.

Among the 11 types of patches, the five natural ones appear to be linked through their shape, size and bathymetric zonation (Fig. A2). The water movement should play an important role and this is true even at the level of the lower limit (Pergent et al., 2014; Vacchi et al., 2012). This hypothesis is supported by the fact that the majority of natural patches encompass a matt cliff facing the shore eroded by the water movement induced by wave action, and a part facing the lower limit recolonized by the surrounding meadow (Blanc and Jeudy De Grissac, 1984; Boudouresque et al., 2012, 1980b). Thus a scenario of the structures succession may be envisaged from the lower to the upper limit of the meadow and/or according to water movement intensity. Given the slow growth rate of P. *oceanica* rhizomes (Di Maida et al, 2013; Gobert et al, 2006), these various types of patches would appear almost motionless at human time scale so the seascapes they form appear not to change. This pattern is in opposition with other seagrass meadows which show seasonal appearances and disappearances of gaps (Bell et al., 1999; Patriquin, 1975).

Conversely, patches generated by anthropogenic activities (trawling, anchoring, bombs, fish farms) modify more rapidly their size and shape through the processes of recolonization or erosion (Francour et al., 1999; Kiparissis et al., 2011; Meinesz and Lefèvre, 1983 ; Pergent-Martini et al., 2006). The natural and anthropogenic patches can be found at the same sites (Calvi, Biguglia) within a short range distance and often interact. For instance, the trawling tracks (TT) going through the matt cliff of ovoid (OP) and colonized patches (CP) at Biguglia should accelerate the erosion and create a corridor in the recolonized part, thus modifying the substrate nature and the faunal communities (Sanchez-Jerez and Ramos Esplá, 1996).

Considering the bare mat (BM) areas it is hard to settle their origin (Moreno et al, 2001) using their shape and size only. However it is possible to determine it according to their location, like the anthropogenic ones near a sewage dredging (Pergent-Martini et al., 1995).

4.2. Metrics relevance

The landscapes indices advised by Sleeman et al. (2005) to investigate the patchiness of seagrass meadows look as being relevant in the study of the patches arrangement in *P. oceanica* meadows except for the division index (DIVISION). Thus, even if DIVISION loadings are strong (≥ 0.3 or ≤ -0.3) at the patch type level (Table 4), this metric does not vary enough in this study to describe patch class impact. This aspect is explained by its definition and the parameters this index encompasses (Table A2).

The Relative wave Exposure Index (REI) seems not informative enough at the scale of the type of patches. It does not encompass in its computation the depth (Infantes et al., 2009), a very important factor in the case of the seagrasses (Sundblad et al., 2014; van Katwijk and Hermus, 2000). It is nevertheless interesting to notice that the bathymétrie succession of natural structures was mainly observed in sites were the REI was high, i.e. Biguglia, Urbinu and Calvi. Water movement being one of the main driver of fragmentation in seagrass meadows (Koch et al, 2006), more sensitive tools with the same easiness of use than the REI must be developed.

Fig. 4. Biplot of the principal components analysis (PCA) showing variations in landscape characteristics for the five sites studied according to the metrics selected (red lines). The percentage reflects the proportion of variance expressed by each axe. Ajaccio:◇; Calvi:△; the South of Macinaggio:○; Biguglia:+; Urbinu:□.
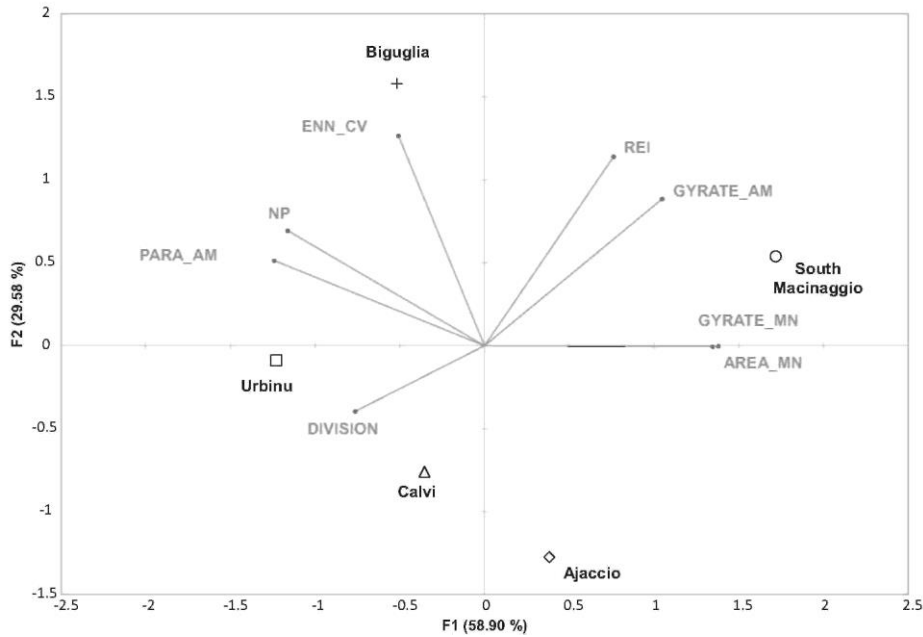

Fig. 5. Biplot of the principal components analysis (PCA) of the metrics selected at the class level for the five sites studied. The percentage reflects the proportion of variance expressed by each axe. ap: anchoring patches: at: anchoring tracks: bi: bomb impact: ffp: fish farm patches: ssp: small sand patches: tt: trawling tracks: lsp: large sand patches: cal: Calvi (△): mac: the South of Macinaggio (○); big: Biguglia (+); aja: Ajaccio (◇); urb: Urbinu (□).
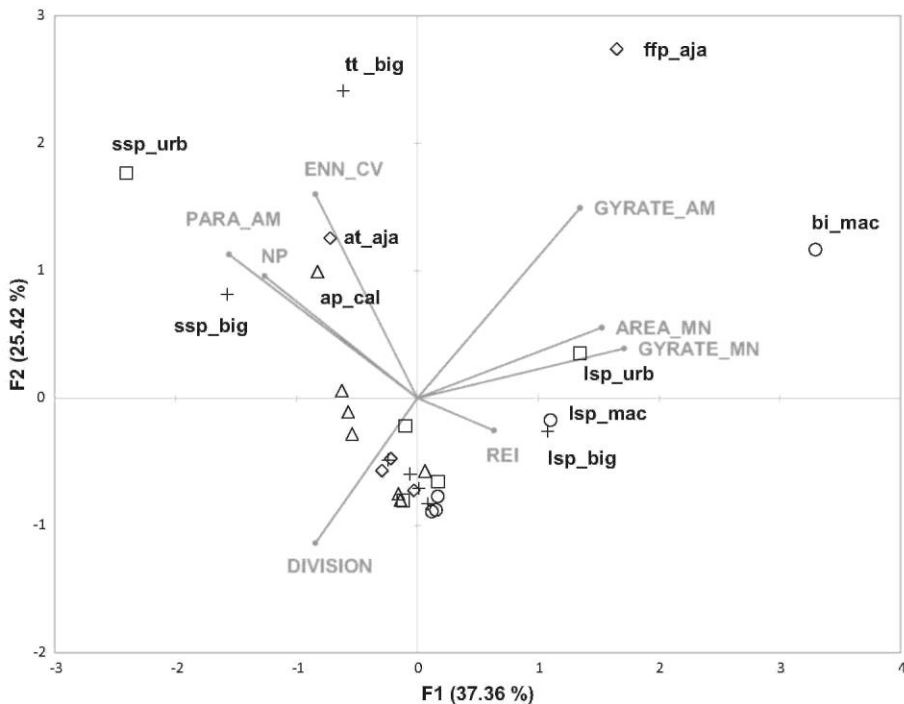
Table 4: principal components analysis (PCA) eigenvalues and variable loadings for the selected indices at the landscape and the patch type scale. Variables in bold are considered strong ($\geq$0.3 or $\leq$-0.3).

	Axis 1	Axis 2
Seascape level		
Eigenvalues	4.77	1.81
Percentage of variance	59.65	22.67
Cumulative percentage of variance	59.65	82.32
Variable loadings		
NP	**0.38**	**0.32**
AREA_MN	**-0.45**	0.00
GYRATE_MN	**-0.46**	0.00
GYRATE_AM	**-0.35**	**0.41**
PARA_AM	**0.41**	0.24
ENN_CV	0.17	**0.59**
DIVISION	0.25	-0.18
REI	-0.25	**0.53**
Class level		
Eigenvalues	8.50	6.32
Percentage of variance	35.65	25.93
Cumulative percentage of variance	35.65	61.58
Variable loadings		
NP	**-0.30**	**-0.36**
AREA_MN	**0.48**	-0.15
GYRATE_MN	**0.50**	-0.12
GYRATE_AM	**0.37**	**-0.49**
PARA_AM	**-0.40**	**-0.42**
ENN_CV	-0.20	**-0.56**
DIVISION	-0.25	**0.32**
REI	0.19	0.02

4.3. The Patchiness Source Index (PaSI)

The list of patches used to calculate the Patchiness Source Index (PaSI) is not exhaustive and can be modified according to the area studied. The bare mats ought to be associated with the natural or anthropogenic patches when their origin can be determined. In practical view, maps used for the calculation of the PaSI require more time of treatment because of the need of identifying at least the origin of each patch. This is why this index is more suitable for a use at a lesser or the same scale than in the present study i.e. on an area of several km². Although describing one aspect of the patchiness in P. *oceanica* meadows, this index does not make any assessment of its degree, other metrics being already available for this task (Montefalcone et al., 2006a, 2010; Moreno et al., 2001). It does not reflect the intensity of the human impact neither. Finally, this index may also be applied on other seagrass meadows presenting both natural and anthropogenic patches.

5. Conclusion

The high resolution of side scan sonar images allows to study patches nature in P. *oceanica* meadows at a large scale and to investigate seascapes features. The different types of patches making up the meadows ought to lead to different P. *oceanica* seascapes according to their shape and their arrangement between one another. Their classification in accordance with landscape metrics leads to the assessment of the main origin (natural or anthropogenic) of the meadow patchiness for a given site. Patches should evolve at various speeds according to their origin, class and the impact of human activities. They are thus an important component in the functioning

of the ecosystem based on P. *oceanica* meadows providing a wide variety of habitats. This approach, the examination of the seascapes structure, is only the first part of a study in the field of landscape ecology which also takes an interest in the function and the changes (Sleeman et al, 2005; Turner, 1989).

The fragmentation (the evolution of patchiness) of the meadows leading to contrasted and complex P. *oceanica* seascapes takes place through several mechanisms and spatial scales. A natural long term process induced by water movement (Boudouresque et al., 2012; Vacchi et al., 2012) is thus opposed to an anthropogenic shorter one (Ardizzone et al., 2006). The anthropogenic process show also different rates of fragmentation according to the type of impact, e.g. physical damages (anchoring, trawling) fragment the meadow more quickly than pollution. Nevertheless this establishment should be modified in a near future. In the case of the natural patches, global climate changes and the increase of extreme events like storms could boost the erosion of the meadows (Pergent et al., 2014). That is why a better understanding at a small scale of the natural patches dynamic (e.g. chemical processes in sediments, rate of erosion/recolonization) could bring a new light on the evolution of P. *oceanica* seascapes. Likewise, seascapes characteristics should be encompassed in indices that aim to assess the quality of the environment, these metrics being now interested in the whole functioning of the ecosystem based on P. *oceanica* meadows (Personnic et al., 2014).

Appendix A.

Fig. A1. Major steps in the study of seagrasses and P. *oceanica* seascapes from 1950 to present days. [1] Molinierand Picard (1952); [2] Losos and Ricklefs(2010); [3] Patriquin (1975); [4] Cristiani (1980); [5] Keddy (1982); [6] synthesis in Boudouresque et al. (2012); [7] Forman and Godron (1986); [8] Turner (1989); [9] Bell and Hicks (1991); [10] Robbins and Bell (1994); [11] Paillard et al. (1993); [12] McGarigal and Marks (1995); [13] Murphey and Fonseca(1995); [14] Pasqualini et al. (1999); [15] Ardizzone et al. (2006); [16] Bell et al. (2006); [17] Boström et al. (2011).
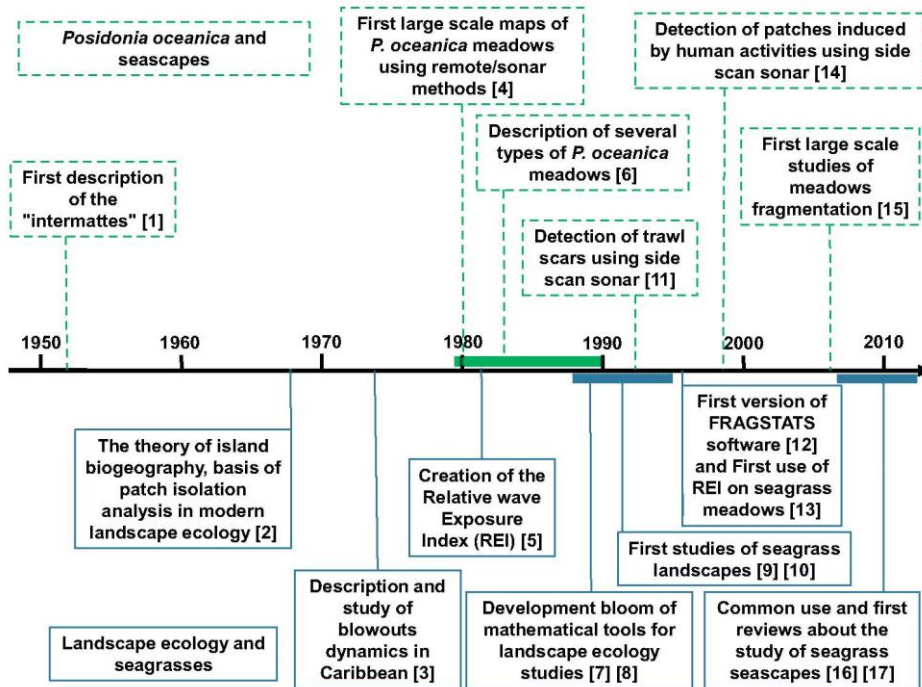

Fig. A2. Diagram of the bathymetric zonation of the different natural patches.
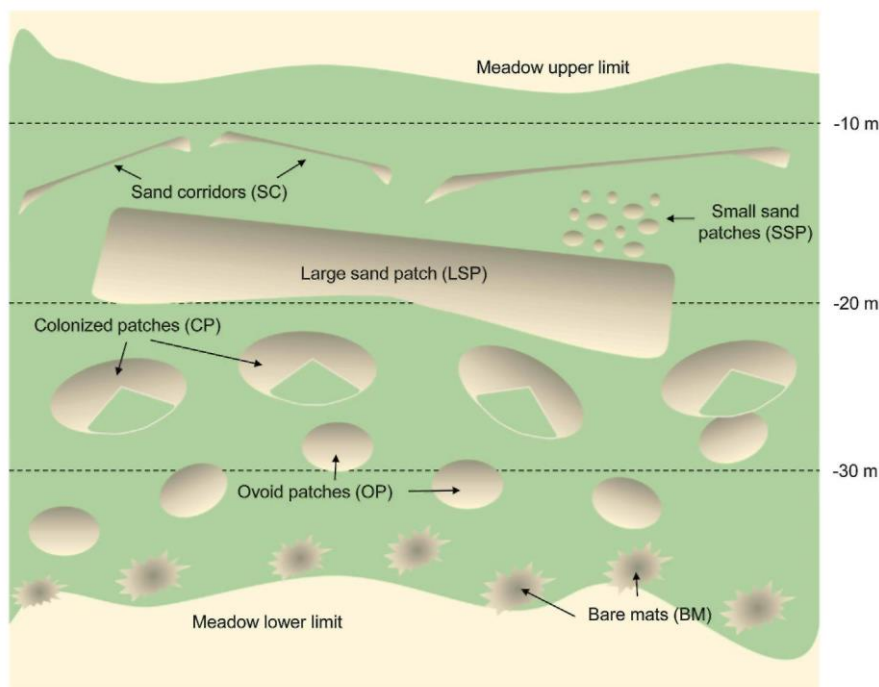
Table A1: Characteristics of the different types of *Posidonia oceanica* meadows described in the past and their designation.

Designation	Description	Reference
Barrier reef	Formation of a barrier due to the vertical growth of *P. oceanica* rhizomes at shallow depth. Creation of a lagoon on the shore side of the barrier	Molinier and Picard (1952)
Erosive intermatte	Sand holes with an ellipsoid shape in a continuous meadow	Molinier and Picard (1952)
Hill meadow	Top erosion by hydrodynamism of a group of *P. oceanica* cuttings surrounded by sand	Boudouresque et al. (1985)
Macro-atolls	Circular patches (>20 m in diameter) of *P. oceanica* at a shallow depth seprated by sand	Pergent et al. (2007)
Micro-atolls	Circular patches of *P. oceanica* (flew meters in diameter) at a shallow depth seprated by sand	Boudouresque et al. (1990)
Plain meadow	Continuous, horizontal or gently sloping meadow, broken by erosive structures	Boudouresque et al. (1980a,b)
Return river	Under a particular orientation of the wind to the coast, channels perpendicular to the shore line can be generated in a continuous meadow	Boudouresque and Meinesz(1982)
Shifting intermatte	Long and narrow corridors parallel to the shore	Boudouresque et al. (1980a,b)
Striped meadow	Strips of *P. oceanica* separated by bare mat	Boudouresque et al. (1990)
Structural intermatte	Small (several dozen of centimeters long) natural patches of bare mat in a continuous meadow	Boudouresque et al. (2012)
Sugar loaf meadow	Mounts of mat with living *P. oceanica* on the top	Molinier and Picard (1954)
Tiered meadow	Steps-like patches of *P. oceanica* seperated by bare mat following a soft bottom slope	Boudouresque et al. (2012)
Undulating meadow	Repeated sequences of patches of bare mat in a continuous meadow	Clairefond and Jeudy De Grissac (1979)

Table A2: The seven landscape metrics recommended by Sleeman et al. (2005) and their abbreviation in FRAGSTATS.

Metric name	FRAGSTATS abbreviation	Equation	Unit
Number of patches	NP	-	None
Mean patch area	AREA_MN	-	m^2
Mean radius of gyration	GYRATE_MN	$GYRATE\_MN = \frac{1}{n} * \sum_{i=1}^{n} \sqrt{(x_i - (x))^2 + (yi - (y))^2}$	m
Area-weighted radius of gyration	GYRATE_AM	$GYRATE\_AM = \frac{\sum_{s=1}^{m}(nsRs)}{\sum_{s=1}^{m}(n_s)}$	m
Coefficient of variation of the Euclidean nearest-neighbor distance	ENNXV	$ENN\_CV = \frac{\sqrt{\frac{\sum_{i=1}^{i=NP} h_i - (\frac{\sum_{i=1}^{i=NP} h_i)}{NP})}{NP}}}{\frac{\sum_{i=1}^{i=NP} h_i}{NP}} * 100$	%
Area-weighted perimeter-area ratio	PARA_AM	$PARA\_AM = \frac{\sum_{i=1}^{i=NP}\frac{p_i}{a_i}a_i}{\sum_{i=1}^{i=NP}\frac{p_i}{a_i}a_i}$	None
Landscape division Index	DIVISION	$DIVISION = \left[1 - \sum_{i=1}^{n}\left(\frac{a_i}{A}\right)^2\right]$	None
Patch density	PD	-	None

References

Ardizzone, G., Belluscio, A., Maiorano, L., 2006. Long-term change in the structure of a *Posidonia oceanica* landscape and its reference fora monitoring plan. Mar. Ecol. 27, 299-309.

Bell, S.S., Brooks, R.A., Robbins, B.D., Fonseca, M.S., Hall, M.O., 2001. Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation.

Biol. Conserv. 100,115-123. Bell, S.S., Fonseca, M.S., Stafford, N.B., 2006. Seagrass ecology: new contributions from a landscape perspective. In: Larkum, A.W.D., Orth, R.J., Duarte, CM. (Eds.), Seagrasses: biology, ecology and conservation. Springer, Netherlands, pp. 625-645.

Bell, S.S., Hicks, G.R.F., 1991. Marine landscapes and faunal recruitment: a field test with seagrasses and copepods. Mar. Ecol. Prog. Ser. 73, 61-68.

Bell, S.S., Robbins, B.D., Jensen, S.L., 1999. Gap dynamics in a seagrass landscape. Ecosystems 2,493-504.

Blanc, J.J., Jeudy De Grissac, A., 1984. Erosion sous-marine des herbiers à Posidonia oceanica (Méditerranée). In: Boudouresque, CF., Jeudy De Grissac, A., Olivier, J. (Eds.), International Workshop on Posidonia oceanica Beds. G.I.S. Posidonie, France, pp. 23-28.

Bonacorsi, M., Pergent-Martini, C, Breand, N., Pergent, G., 2013. Is *Posidonia oceanica* regression a general feature in the Mediterranean Sea? Mediterr. Mar. Sci. 14, 193-203.

Borg, J.A., Rowden, A.A., Attrill, M.J., Schembri, P.J., Jones, M.B., 2006. Wanted dead or alive: high diversity of macroinvertebrates associated with living and 'dead' *Posidonia oceanica* matte. Mar. Biol., 667-677.

Boström, C, Jackson, E.L., Simenstad, C.A., 2006. Seagrass landscapes and their effects on associated fauna: A review. Estuarine. Coast. Shelf Sci. 68, 383-403.

Boström, C, Pittman, S.J., Simenstad, C.A., Kneib, R.T., 2011. Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. Mar. Ecol. Prog. Ser. 427,191-217.

Boudouresque, CF., Bernard, G., Bonhomme, P., Charbonnel, E., Diviacco, G., Meinesz, A., Pergent, G., Pergent-Martini, C, Ruitton, S., Tunesi, L., 2012. Protection and conservation of *Posidonia oceanica* meadows. RAMOGE Pub., Tunis, pp. 202.

Boudouresque, CF., Bernard, G., Pergent, G., Shili, A., Verlaque, M., 2009. Regression of Mediterranean seagrasses caused by natural processes and anthropogenic disturbances and stress: a critical review. Bot. Mar. 52, 395-418.

Boudouresque, CF., Bianconi, C.H., Meinesz, A., 1990. Live *Posidonia oceanica* in a corraligenous algal bank at Sulana Bay, Corsica Rapports et PV des réunions de la Commission Internationale pour l'Exploration Scientifique de la Méditerranée 32., pp. 11.

Boudouresque, CF., Giraud, G., Panayotidis, P., 1980a. Végétation marine de l'île de Port-Cros (parc National) XIX: mise en place d'un transect permanent. Travaux Scientifiques du Parc National de Port-Cros 6., pp. 207-221.

Boudouresque, CF., Jeudy De Grissac, A., Meinesz, A., 1985. Un nouveau type d'herbier à Posidonia oceanica: l'herbier de colline. Rapports et PV des réunions de la Commission Internationale pour l'Exploration Scientifique de la Méditerranée 29., pp. 173-175.

Boudouresque, CF., Meinesz, A., 1982. Découverte de l'herbier de posidonie. Cahier Parc National Port-Cros 4, France, pp. 1-79.

Boudouresque, CF., Thommeret, J., Thommeret, Y., 1980b. Sur la découverte d'un bioconcrétionnement fossile intercalé dans l'herbier à Posidonia oceanica de la baie de Calvi (Corse), Journées d'Etude de Systématique et Biogéographie méditerranéenne. CIESM Pub., Cagliari, pp. 139-142.

Clairefond, P., Jeudy De Grissac, A., 1979. Description et analyse des structures sédi-mentaires en milieu marin: recensement de quelques exemples dans l'herbier de Posidonies autour de l'île de Port-Cros (Parc national). Travaux Scientifiques du Parc National de Port-Cros 5., pp. 79-104.

Connolly, R.M., Hindell, J.S., 2006. Review of nekton patterns and ecological processes in seagrass landscapes. Estuar. Coast. Shelf Sci. 68,433-444.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, It, Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253-260.

Cristiani, G., 1980. Biomasse et répartition de l'herbier de Posidonia oceanica de la Côte Bleue (B. d. Rh. France) et pollution marine par les métaux lourds. Univ. Aix-Marseille 3, pp. 150.

Di Maida, G., Tomasello, A., Sciandra, M., Pirrotta, M., Milazzo, M., Calvo, S., 2013. Effect of different substrata on rhizome growth, leaf biometry and shoot density of *Posidonia oceanica.* Mar. Environ. Res. 87-88, 96-102.

Fonseca, M.S., Bell, S.S., 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Mar. Ecol. Prog. Ser. 171, 109-121.

Forman, R.T.T., Godron, M., 1986. Landscape Ecology. John Wiley, New York, pp. 1-619.

Francour, P., Ganteaume, A., Poulain, M., 1999. Effects of boat anchoring in *Posidonia oceanica* seagrass buds in the Port-Cros National Park (Northwestern Mediterranean Sea). Aquat. Conserv.: Mar. Freshw. Ecosyst. 9, 391-400.

Ginsburg, R.N., 1956. Environmental relationships of grain size and constituent particles in some South Florida carbonate sediments. Bull. Am. Assoc. Petrol. Geol. 40, 2384-2427.

Gobert, S., Cambridge, MX., Velimirov, B., Pergent, G., Lepoint, G., Bouquegneau, J.M., Dauby, P., Pergent-Martini, C, Walker, D.I., 2006. Biology of Posido-nia, Seagrasses: Biology, Ecology, and Conservation. Springer, Dordrecht, The Netherlands, pp. 387-408.

Gobert, S., Chéry, A., Volpon, A., Pelaprat, C, Lejeune, P., 2014. The Seascape as an indicator of environmental interest and quality of the Mediterranean benthos: the in situ development of a description index: the LIMA. In: Musard, O., Le Dû-Blayo, L., Francour, P., Beurier, J.P., Feunteun, E., Talassinos, L. (Eds.), Underwater Seascapes. Springer International Publishing, Switzerland, pp. 277-291.

Infantes, E., Terrados, J., Orfila, A., Canellas, B., Álvarez-Ellacuria, A., 2009. Wave energy and the upper depth limit distribution of *Posidonia oceanica.* Bot. Mar. 52, 419-427.

Keddy, P.A., 1982. Quantifying within-lake gradients of wave energy: interrelationships of wave energy, substrate particle size and shoreline plants in axe lake, Ontario. Aquat. Bot. 14, 41-58.

Kiparissis, S., Fakiris, E., Papatheodorou, G., Geraga, M., Kornaros, M., Kapareliotis, A., Ferentinos, G., 2011. Illegal trawling and induced invasive algal spread as collaborative factors in a *Posidonia oceanica* meadow degradation. Biol. Invasions 13, 669-678.

Koch, E., Ackerman, J.D., Verduin, J., van Keulen, M., 2006. Fluid dynamics in seagrass ecology—from molecules to ecosystems. In: Larkum, A.W.D., Orth, R.J., Duarte, CM. (Eds.), Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht, The Netherlands, pp. 196-225.

Leriche, A., Pasqualini, V., Boudouresque, CF., Bernard, G., Bonhomme, P., Clabaut, P., Denis, J., 2006. Spatial, temporal and structural variations of ^*Posidonia oceanica* seagrass meadow facing human activities. Aquat. Bot. 84, 287-293.

Li, X., Mander, U., 2009. Future options in landscape ecology: development and research. Prog. Phys. Geogr. 33,31-48.

Losos, J.B., Ricklefs, R.E., 2010. The Theory of Island Biogeography Revisited. Princeton University Press, Princeton, pp. 495-499.

McGarigal, It, Cushman, S.A., Ene, E., 2014. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Amherst, Computer software program produced by the authors at the University of Massachusetts.

McGarigal, It, Marks, B.J., 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure, Gen. Tech. Report PNW-GTR-351. USDA Forest Service, Pacific Northwest Research Station, Portland, USA.

Meinesz, A., Lefèvre, J.R., 1983. Régénération d'un herbier à Posidonia oceanica quarante années après sa destruction par une bombe dans la rade de Villefranche (Alpes-Maritimes). In: Boudouresque, CF., Jeudy De Grissac, A., Olivier, J. (Eds.), International Workshop on Posidonia oceanica Beds. G.I.S. Posidonie, Marseille, France, pp. 39-44.

Micheli, F., Peterson, C.H., 1999. Estuarine vegetated habitats as corridors for predator movements. Conserv. Biol. 13, 869-881.

Molinier, R., Picard, J., 1952. Recherches sur les herbiers de phanérogames marines du littoral méditerranéen français. Ann. lTnst. Océanogr. 27,157-234.

Molinier, R., Picard, J., 1954. Eléments de bionomie marine sur les côtes de Tunisie. Bull. Station Océanogr. Salammbô 48,3-47.

Montefalcone, M., Albertelli, G., Bianchi, C.N., Mariani, M., Morri, C, 2006a. A new synthetic index and a protocol for monitoring the status of *Posidonia oceanica* meadows: a case study at sanremo (Ligurian Sea, NW Mediterranean). Aquat. Conserv.: Mar. Freshw. Ecosyst. 16, 29-42.

Montefalcone, M., Lasagna, R., Bianchi, C.N., Morri, C, Albertelli, G., 2006b. Anchoring damage on*Posidonia oceanica* meadow cover: a case study in Prelo cove (Ligurian Sea, NW Mediterranean). Chem. Ecol. 22, S207-S217.

Montefalcone, M., Parravicini, V., Vacchi, M., Albertelli, G., Ferrari, M., Morri, C, Bianchi, C.N., 2010. Human influence on seagrass habitat fragmentation in NW Mediterranean Sea. Estuar. Coast. Shelf Sci. 86, 292-298.

Moreno, D., Aguilera, P.A., Castro, H., 2001. Assessment of the conservation status of seagrass *(Posidonia oceanica)* meadows: implications for monitoring strategy and the decision-making process. Biol. Conserv. 102,325-332.

Murphey, P.L., Fonseca, M.S., 1995. Role of high and low energy seagrass beds as nursery areas for *Penaeus duorarum* in North Carolina. Mar. Ecol. Prog. Ser. 121, 91-98.

Paillard, M., Gravez, V., Clabaut, P., Walker, P., Blanc, J.J., Boudouresque, CF., Belsher, T., Ursheller, F., Poydenot, F., Sinnasammy.J.M., Augris, C, Peyronnet, J.P., Kessler,

M., Augustin, J.M., Le Drezen, E., Prudhomme, C, Raillard, J.M., Pergent, G., Hoareau, A., Charbonel, E., 1993. Cartographie de l'herbier de Posidonie et des fonds marins environnants de Toulon à Hyères (Var-France). Reconnaissance par sonar latéral et photographie aérienne. Notice de présentation, Marseille, pp. 36.

Pasqualini, V., Pergent-Martini, C, Pergent, G., 1999. Environmental impact identification along the Corsican coast (Mediterranean sea) using image processing. Aquat. Bot 65, 311-320.

Patriquin, D.G., 1975. Migration of blowouts in seagrass beds at Barbados and Carri-acou, West Indies, and its ecological and geological implications. Aquat. Bot. 1, 163-189.

Pergent-Martini, C, Boudouresque, CF., Pasqualini, V., Pergent, G., 2006. Impact of Ash farming facilities on *Posidonia oceanica* meadows: a review. Mar. Ecol. 27, 310-319.

Pergent-Martini, C, Pasqualini, V., Pergent, G., 1995. Monitoring of the *Posidonia oceanica* meadow in proximity of the sea outfall from the sewage treatment plant at Marseille (Mediterranean, France). EARSeL Adv. Rem. Sens. 4, 128-134.

Pergent, G., Bazairi, H., Bianchi, C.N., Boudouresque, CF., Buia, M.C, Calvo, S., Clabaut, P., Harmelin-Vivien, M., Mateo, M.A., Montefalcone, M., Morri, C, Orfanidis, S., Pergent-Martini, C, Semroud, R., Serrano, O., Thibaut, T., Tomasello, A., Verlaque, M., 2014. Climate change and Mediterranean seagrass meadows: a synoPaSIs for environmental managers. Mediterr. Mar. Sci. 15, 462-473.

Pergent, G., Djellouli, A., Hamza, A.A., Ettayeb, K.S., Alkekli, A., Talha, M., Alkunti, E., 2007. Structure of Posidonia oceanica meadows in the vicinity of Ain al-Ghazala lagoon (Libya): the « macroatoll » ecomorphosis. In: Pergent-Martini, C, EI Asmi, S., Le Ravallec, C. (Eds.), Third Mediterranean symposium on marine vegetation. RAC/SPA Publ., Marseilles, pp. 135-140.

Pergent, G., Pergent-Martini, C, Boudouresque, CF., 2013. Trawling Impacts on Mediterranean Seagrass. Seagrass-Watch, pp. 26-30.

Personnic, S., Boudouresque, CF., Astruch, P., Ballesteros, E., Blouet, S., Bellan-Santini, D., Bonhomme, P., Thibault-Botha, D., Feunteun, E., Harmelin-Vivien, M., Pergent, G., Pergent-Martini, C, Pastor, J., Poggiale, J.C Renaud, F., Thibaut, T., Ruitton, S., 2014. An ecosystem-based approach to assess the status of a mediterranean ecosystem, the *Posidonia oceanica* seagrass meadow. PLoS ONE 9, e98994.

Prado, P., Alcoverro, T., Romero, J., 2009. Welcome mats? The role of seagrass meadow structure in controlling post-settlement survival in a keystone sea-urchin species. Estuar. Coast. Shelf Sci. 85,472-478.

Robbins, B.D., Bell, S.S., 1994. Seagrass landscapes: a terrestrial approach to the marine subtidal environment. Trends Ecol. Evol. 9,301-304.

Ruíz, J.M., Boudouresque, CF., Enriquez, S., 2009. Mediterranean seagrasses. Bot. Mar. 52,369-381.

Sánchez-Jerez, P., Ramos Esplá, A.A., 1996. Detection of environmental impacts by bottom trawling on *Posidonia oceanica* (L.) Delile meadows: sensitivity of fish and macroinvertebrate communities. J. Aquat. Ecosyst. Health 5, 239-253.

Sleeman, J.C, Kendrick, G.A., Boggs, G.S., Hegge, B.J., 2005. Measuring fragmentation of seagrass landscapes: which indices are most appropriate for detecting change? Mar. Freshw. Res. 56, 851-864.

Sousa,W.P., 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology 65,1918-1935.

Sundblad, G., Bekkby, T., Isæus, M., Nikolopoulos, A., Norderhaug, K.M., Rinde, E., 2014. Comparing the ecological relevance of four wave exposure models. Estuar. Coast. Shelf Sci. 140, 7-13.

Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. Evol. Syst. 20, 171-197.

Vacchi, M., Montefalcone, M., Bianchi, C.N., Morri, C, Ferrari, M., 2012. Hydro-dynamic constraints to the seaward development of *Posidonia oceanica* meadows. Estuar. Coast. Shelf Sci. 97,58-65.

van Katwijk, M.M., Hermus, D.C.R., 2000. Effects of water dynamics on *Zostera marina:* transplantation experiments in the intertidal Dutch Wadden Sea. Mar. Ecol. Prog. Ser. 208,107-118.

Vassallo, P., Paoli, C, Rovere, A., Montefalcone, M., Morri, C, Bianchi, C.N., 2013. The value of the seagrass *Posidonia oceanica:* a natural capital assessment. Mar. Pollut. Bull. 75,157-167.