Temporal evolution of sand corridors in a *Posidonia oceanica* seascape: a 15-year study

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Abstract

The spatial dynamics of the *Posidonia oceanica* meadows is a process extending over centuries. This article shows evidence of the natural dynamics of the *P. oceanica* "shifting intermattes" or "sand corridors" (hereafter SCs) – unvegetated patches within a dense meadow. We have studied the features and temporal evolution (2001–2015) of five SCs in the Calvi Bay (Corsica) at a 15 m depth and followed the characteristics of the *P. oceanica* meadow lining the edge of patches. All SCs show a similar morphology. The eroded side has a vertical edge where roots, rhizomes, and sediments are visible, whereas, on the opposite colonized side, the sand is at the same level as the continuous meadow. The vertical edge reaches a maximum height of 160 cm and is eroded by orbital bottom currents with a maximum speed of 12 cm.s^{-1}– the erosion speed ranging from 0.6 to 15 cm.a^{-1}. SCs progress toward the coastline with a mean speed of 10 cm.a^{-1}. The rate of colonization by the *P. oceanica* shoots ranges from 1.5 to 21 cm.a^{-1}. We have calculated that the studied SCs will reach the coastline within 500 to 600 years. We finally discuss the implication of such dynamics in the framework of the assessment of meadow colonization and the seascape dynamics.

Keywords: Seagrass colonization, *Posidonia oceanica* dynamics, Intermatte, Mediterranean Sea, Seascape.

Introduction

The endemic species, *Posidonia oceanica* (L.) Delile is the main seagrass of the Mediterranean Sea. This plant forms extensive meadows from the surface to a depth of 40 m considered as "climax" habitats (Boudouresque *et al.*, 2012; Pergent *et al.*, 2012).Over the last three decades the interest in landscape ecology has grown and spread from land to marine ecosystems (Bell *et al.*, 2006) and *P. oceanica* meadows (Montefalcone *et al.*, 2013) to assess the conservation state of coastal areas. At present, the morphology of meadows, such as, the presence and arrangement of bare patches (e.g.*,* natural or anthropogenic bare mattes and intermattes) are used as characteristic imprints of environmental conditions (Pergent *et al.*, 1995; Montefalcone, 2009; Montefalcone *et al.* 2010, Abadie *et al.*, 2015). Landscape tools are being widely utilized in the study of seagrass meadows (seascapes), but still require the establishment of several bases. More precisely, patch descriptions and their temporal evolution must be investigated to sort out the natural erosion from the anthropogenic erosion of *P. oceanica* meadows.

Among the patches, special focus has been laid on a particular structure called "shifting intermattes" or "sand corridors" (SCs), that is, a sand patch within a *P. oceanica* meadow, described 60 years ago by Molinier & Picard (1952). This patch type displays an interesting structural particularity for study of the erosive and colonization processes of the meadows. On one side, the currents at

the bottom erode the meadow creating a vertical edge of matte, whereas, on the other side *P. oceanica* colonizes the bare sandy bottom (Boudouresque *et al.*, 1980).

To follow the spatial evolution of *P. oceanica* meadows and patch generation on a small scale, several non-destructive methods have been developed, for example*,* the permanent square (Noël *et al.*, 2012) and acoustic telemetry (Descamp *et al.*, 2011). Another method to assess the ability of *P. oceanica* to colonize bare substrates consists of measuring rhizome elongation using lepidochronology, that is, the annual cycles of scale thickness (Pergent *et al.*, 1989). However, these methods remain time consuming, expensive, and destructive. Thus, the present work, through the long-term study of the SCs' particularities, aims to (1) propose a non-destructive and cost-effective method to assess their spatial evolution, (2) describe the dynamics of natural patches inside the *P. oceanica* meadows, and (3) discuss its implication for the whole *P. oceanica* seascape.

Materials and Methods

This study took place in the Calvi Bay, located in the Mediterranean Sea, on the northwest coast of Corsica (42.583333 N, 8.750000 E; Fig. 1), a nutrient-poor (ultra-oligotrophic) and pristine area. *P. oceanica* is the dominant macrophyte species found at the bottom of that bay and covers the sandy and rocky substrata. Its lower

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limit reaches a depth of 38 m (Bay, 1984). Despite these very low nutrient concentrations, the meadow displays both high biomass and productivity (more than 500 $g_{DW}.m^{-2}.y^{-1}$); *P. oceanica* beds are thus considered as Low Nutrient–High Chlorophyll (LNHC) systems (Gobert *et al.*, 2002). The meadow in the studied bay is qualified as healthy (Gobert *et al.*, 2009) and no significant changes in its vitality have been registered since 1975 (Jousseaume *et al.*, 2014).

The study was carried out from July 2001 to June 2015 on the SCs (Fig. 1) located in front of the research station of STARESO (STAtion de REcherches Sous marines et Océanographiques) between 13 m and 16 m in depth, resulting in a 15-year temporal survey. In July 2001, the borders of five patches were marked out with labeled pegs, anchored 50 cm deep in the sediments. A map was then obtained using triangulation measurements between pegs. This first delimitation was left in place and a same marking process was performed in June 2002 and in June 2003. The distance between each peg was recorded in June 2002 (evolution from 2001 to 2002) and in June 2003 (evolution from 2002 to 2003). In June 2010 and 2015, the relative position of the pegs was again measured on patch 2 (Fig. 1).

In September 2001, four sediment cores (diameter of 5 cm) were sampled in the middle of patch 5 and in the adjacent continuous *P. oceanica* meadow. The mean length of the sediment cores was approximately 10 cm. Grain size (fine silt to coarse sand) was measured using sieves of 0.8, 0.4, 0.2, 0.1, 0.05, 0.025, and 0.0125 mm.
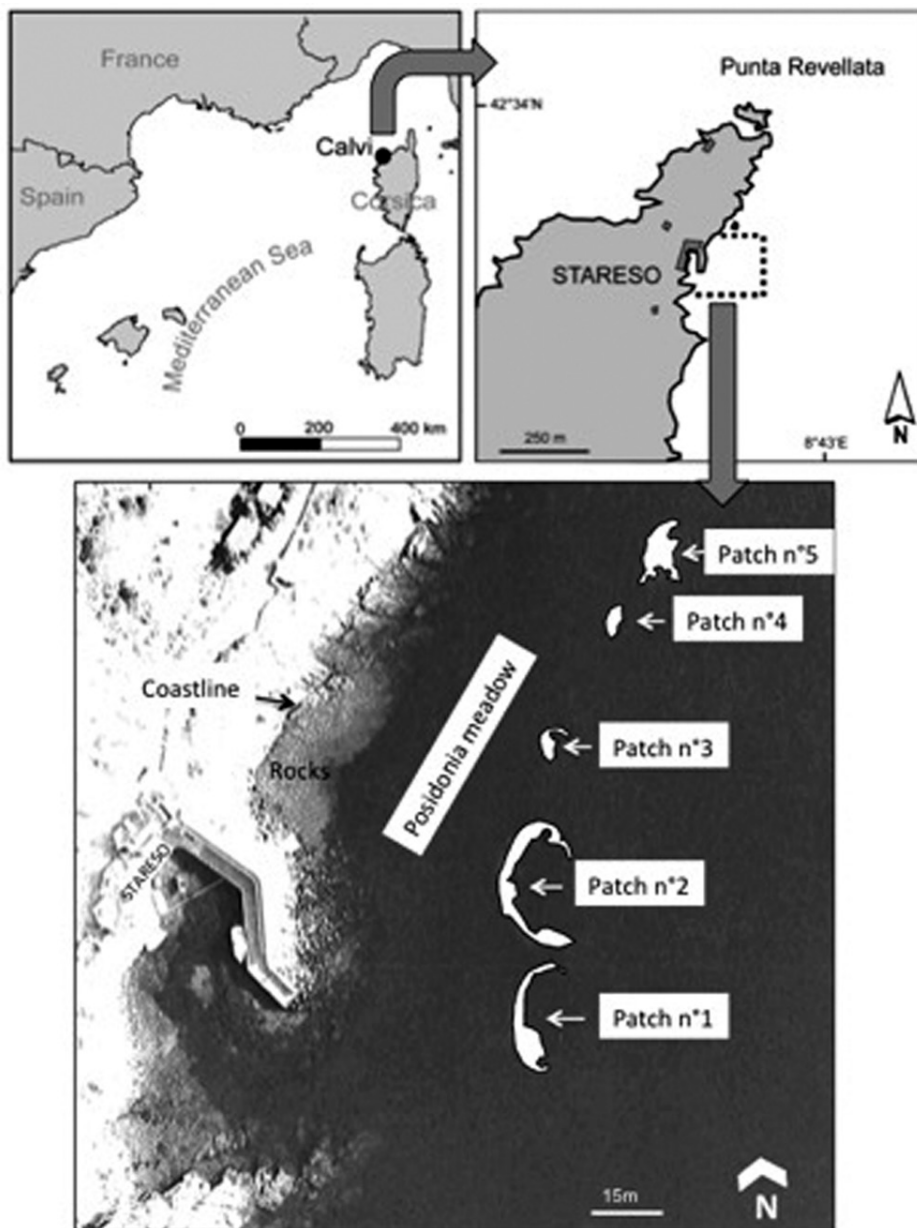

Fig. 1: Study site in front of STARESO in the Calvi Bay (Corsica): Sand corridors forming a row of five sand patches in the *P. oceanica* meadow.

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Each fraction was dried for 48 hours at 60°C and was weighed before and after drying. Sediments were classified according to their grain size, using the scale of Wentworth (1922).

The speed and direction of the currents at the bottom were measured from November 2001 to October 2002 using an Aanderaa™ RCM7 current meter placed within patch 1 close to the eroded side. The current speed and its direction were measured every 20 minutes and the data were retrieved each month.

The morphological transects of patches were performed from 2001 to 2003 (description and measurement). Within the same period, the shoot density and the number of creeping (plagiotropic) and erect (orthotropic) shoots were counted in the surrounding meadow near the patches (on both the eroded and colonized sides), by using a square of 40 cm x 40 cm (n = 16) (Soullard *et al.*, 1994). Furthermore, one plagiotropic rhizome from each patch's colonized side was sampled in July 2015, to measure the mean annual growth, thanks to lepidochronology (Pergent *et al.*, 1989).

Results

The five SCs are aligned one after the other parallel to the coast. The shape of patches 1 and 2 can be compared to a banana; patches 3 and 4 display a reduced area in comparison to the other three, and the outline of patch 5 is more serrated (Fig. 1). All patches show a similar morphology. The eroded side (landward) is a vertical edge facing west, in which the roots, rhizomes, and sediments forming the matte are visible (Fig. 2a). The maximum height of the edge of up to 160 cm (patch 2), is at the mid length of the eroded side and decreases toward the patch's extremities. It can be described as a sheer vertical matte or a beetling scarp (Fig. 2). At the colonized side (seaward), the sand is at the same level as the continuous meadow and the matte is less thick with plagiotropic rhizomes (Fig. 2b).

In the *P. oceanica* meadow, around 75% of the sediments below a grain-size of 0.8 mm are constituted by grains smaller than 0.1 mm, that is, silt, while in the SC, this proportion is only 60% (Table 1). On the eroded side the sediments are fine (Fig. 2a), while at the colonized side the sediments are coarse-grained and composed of organic material and shell fragments (Fig. 2b).

Currents speed varies from 1.00 to 12.14 cm.s^{-1} on the eroded side with a mean value of 1.72 ± 0.69 cm.s^{-1} (Fig. 3a). Currents mainly come from the southeast (39%) and more seldom from the east (17%) and north–west (15%) (Fig. 3b).

The temporal survey of the five patches performed in 2002 and 2003 reveals that the mean erosion of the vertical edge does not differ from one patch to another, that is, between 19.5 ± 13.9 and 24.4 ± 12.2 cm.a^{-1} from 2001 to 2002 and between 5.4 ± 3.3 and 11.8 ± 7.0 cm.a^{-1} from 2002 to 2003 (Table 2). However, the mean erosion has
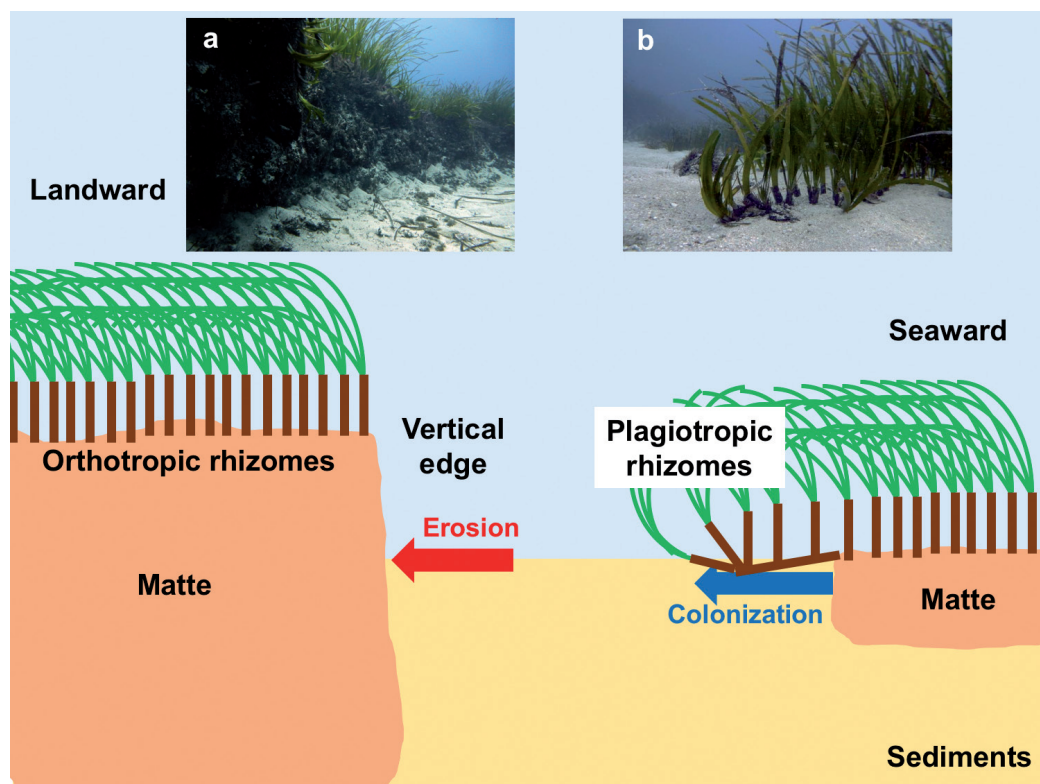

Fig. 2: Schematic representation of a sand corridor with pictures of, (a) the eroded side; (b) the colonized side (photos a and b: A. Abadie).

Table 1. Percentage of each granulometric fraction according to the sieve meshing and the classification of Wentworth (1922).

	Sand				Silt			
Granulometry	Coarse	Medium	Fine	Very fine	Coarse	Medium	Fine	
Sieve size (mm)	**0.8**	**0.4**	**0.2**	**0.1**	**0.05**	**0.025**	**0.0125**	**< 0.0125**
SCsample 1	0.6	2.0	9.8	28.2	39.3	17.0	2.6	0.5
SCsample 2	0.6	4.3	6.6	23.5	40.2	17.6	4.9	2.4
Meadow sample 1	0.5	0.5	4.8	18.3	34.2	30.7	8.3	2.9
Meadow sample 2	0.7	1.1	6.0	18.8	41.4	22.5	6.6	3.0

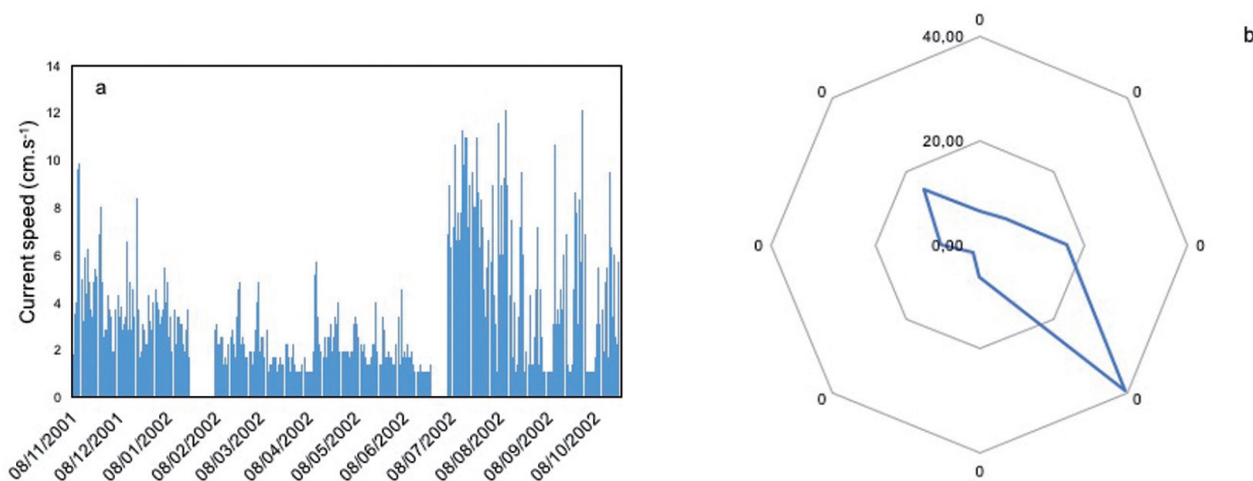**Fig. 3:** (a) Current speed (cm.s^{-1}) from November 2001 to October 2002 at patch 1 near the vertical edge; (b) current frequency (%) according to their cardinal source.

been significantly higher from 2001 to 2002 (22.8 cm.a^{-1}) in comparison to the 2002–2003 period (9.0 cm.a^{-1}). The long-term survey of spatial dynamics of patch 2 between 2001 and 2015 shows erosion of its vertical edge ranging between 50 and 135 cm for the 15-year time interval and a colonization ranging from 14 to 190 cm (Table 2). The lepidochronological analysis of rhizome length revealed the past growth back to 2007 for patch 4, back to 2008 for patches 2 and 3, back to 2009 for patch 1, and back to 2011 for patch 5. Plagiotropic rhizomes show relatively homogeneous mean annual growth rates between the five patches, ranging from 3.2 to 4.5 cm.a^{-1}. Strong knots of roots have been observed at the extremities of plagiotropic rhizomes (Fig. 4). At the top of the vertical edge in patch 2 (13 m depth), the mean density of the *P. oceanica* meadow is 403 ± 203 shoots.m^{-2} (with 9% of plagiotropic rhizomes). On the colonized side (15 m depth), the mean density reaches 229 ± 58 shoots.m^{-2} (with 21% of plagiotropic rhizomes).

Discussion

The SCs studied here are natural structures eroded by water movements (Boudouresque & Meinesz, 1982; Blanc & Jeudy De Grissac, 1984), embedded in a whole *P. oceanica* seascape structured by wave energy at a shal-

low depth (Infantes *et al.*, 2009, Vacchi *et al.*, 2010). Our work aims to characterize the SC dynamics with a temporal approach, to provide a new insight into the colonization evaluation in the framework of seascape studies.

On the one hand, the mean colonization speed of patches measured, thanks to lepidochronology (rhizome growth of 3.9 cm.a^{-1}), was consistent with the previous data. An average speed of rhizome growth of 3 to 4 cm.a^{-1} was measured by Meinesz & Lefèvre (1984); between 1.0 and 7.0 cm.a^{-1} by Caye (1982); and between 0.4 and 1.1 cm.a^{-1} and between 0.4 and 7.4 cm.a^{-1} for orthotropic and plagiotropic rhizomes, respectively, by Molenaar & Meinesz (1995). On the other hand, the colonization of patches by the *P. oceanica* shoots based on our long-term census (2001–2015) using labeled pegs ranged between 1.0 and 23.5 cm.a^{-1}. The average recolonization speed value (11.0 cm.a^{-1}) was higher than those obtained with lepidochronology.

The present study, therefore, suggests that plagiotropic rhizome elongation, as determined by lepidochronology, does not correspond to the observed longitudinal spreading capacity of the meadow using anchored fixed marks. Our observations (Figs 4 and 5) show that leaves, through their horizontal growth pattern, with a production of primary roots close to their insertion rank basis (Fig. 4), can initiate the colonization process.

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Table 2. Surface area (m²), vertical edge erosion and colonization speed by *P. oceanica* (cm.a⁻¹) at the five SCs. Erosion and colonization data are given as mean ± SD, minimum and maximum values and number of measurements. The mean growth (cm.a⁻¹) of plagiotropic rhizomes for each patch are given as mean ± SD for their respective time interval.

Patch		1	2	3	4	5
Surface area (m²)		104	135	28	24	99
Yearly mean erosion (cm.a⁻¹)						
	2001–2002	24.2 ± 12.0 0-46 18	24.4 ± 12.2 11-45 26	22.4 ± 7.7 10-35 9	23.3 ± 3.2 19-26 7	19.5 ± 13.9 0-56 14
	2002–2003	11.8 ± 7.0 3-31 18	9,4 ± 4.1 3-18 26	9.0 ± 5.3 7-20 9	5.4 ± 3.3 0-8 7	9.7 ± 7.4 0-27 14
	2001–2010		77.0 ± 29.4 50-135 23			
	2014–2015	10.3 ± 8.5 0-19.5 17				
Yearly mean colonization (cm.a⁻¹)						
	2001–2010		98.6 ± 58.1 14-190 14			
	2014–2015	11.1 ± 6.6 1-23.5 29				
Yearly mean plagiotropic rhizomes growth (cm.a⁻¹)		4.1 ± 1.4 2009–2014	3.2 ± 1.2 2008–2014	4.3 ± 0.6 2008–2014	4.5 ± 1.4 2007–2014	3.5 ±0.8 2011–2014

This colonization rate, measured with pegs, further matches the progression rate assessed by the acoustic telemetry along the French coast (Descamp *et al.*, 2011). For colonization assessment of the *P. oceanica* meadows, it is primordial to take into account the advance of the entire meadow, that is, plagiotropic rhizomes as well as their leaves and scales (Fig. 5) and not only rhizome elongation. Therefore, the use of beacons appears well-suited for such monitoring studies. Moreover, the meadow progression measured with this method corresponds to the one assessed with remote sensing, for example, the side scan sonar and satellite images (Descamp *et al.*, 2011, Clabaut *et al.*, 2014).

Looking at the opposite eroding side of the SCs, the temporal evolution of the vertical edges leads to seascape features similar to a beach banquette dynamic of *P. oceanica* leaves, as described by Mateo *et al.* (2003). The process occurs through the removal of sediments from the matte edge and the modification of the sedimentation rate of particles (Folkard, 2005). A diagram of the successional stages of erosion is proposed in figure 6. The base of the vertical edge is eroded leading the *P. oceanica* meadow to hang over the notch. The notch increases and the overhanging meadow then collapses. Debris from the meadow –pieces of matte with living *P. oceanica*– are finally removed or possibly start to grow again.

According to Blanc & Jeudy De Grissac (1984), SCs parallel to the coast depend on drift currents, but the effects of intense storms, even those short in duration, are preponderant. The two main wind sectors in the Calvi Bay are the north-east (Tramontane) and southwest (Libeccio) winds (Skliris & Djenidi 2006), both being powerful enough to generate waves and thus currents are derived at the bottom from wave energy. In the present study, SCs have been subjected to low currents with a maximum recorded speed of 12 cm.s⁻¹ (Fig. 3).

Fig. 4: Plagiotropic rhizome sampled for lepidochronology at the colonized side of patch 4 showing a knotwork of roots at its extremity (photo: S. Gobert).
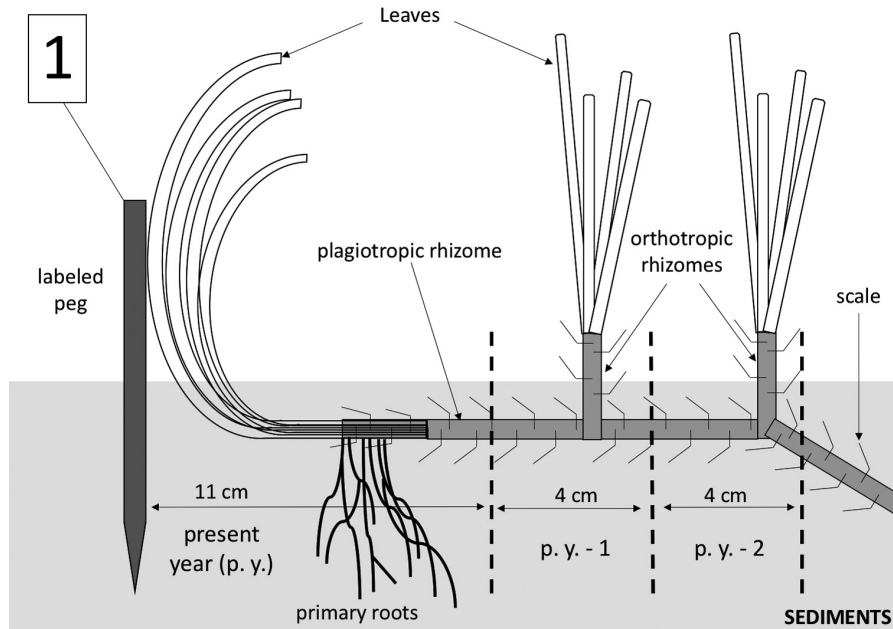
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Fig. 5: Schematic representation of the *P. oceanica* meadow progression encompassing the present year (p. y.) colonization assessed by the labeled peg, and the past rhizome elongation (p. y. -1 and p. y. -2) measured according to lepidochronology.

This maximum current speed is far from the one considered to prevent *P. oceanica* meadow development (about 40 cm.s⁻¹ (Infantes *et al.*, 2009)). However, at the mean depth of the present study (15 m) waves remain capable of generating dead matte areas (Vacchi *et al.*, 2016), their constant erosion activity on the seagrass meadow will possibly lead to SCs.

The mechanical influence of the current speed results in part from the granulometric characteristics of the sediment grains. Sediments of sand patches originate mainly from the erosion of the vertical edge (Cinelli *et al.*, 1995) as well as from the pieces of collapsed living matte (De Falco *et al.*, 2000). At the colonized side of SCs, more plagiotropic shoots are found in the zone of sediments accretion. From the eroded side to the colonized one, the grain size increases, causing the appearance of coarse sediments between the plagiotropic shoots (Fig. 2a-b). Within the surrounding *P. oceanica* meadow, the canopy acts as a sink of particles and reduces the flow velocity (Gacia *et al.*, 1999). Under the relatively low water motion at the bottom of the studied area, the surrounding meadow has a stabilization influence on nearby SC sediments (Stratigaki *et al.*, 2011, Manca *et al.*, 2012).
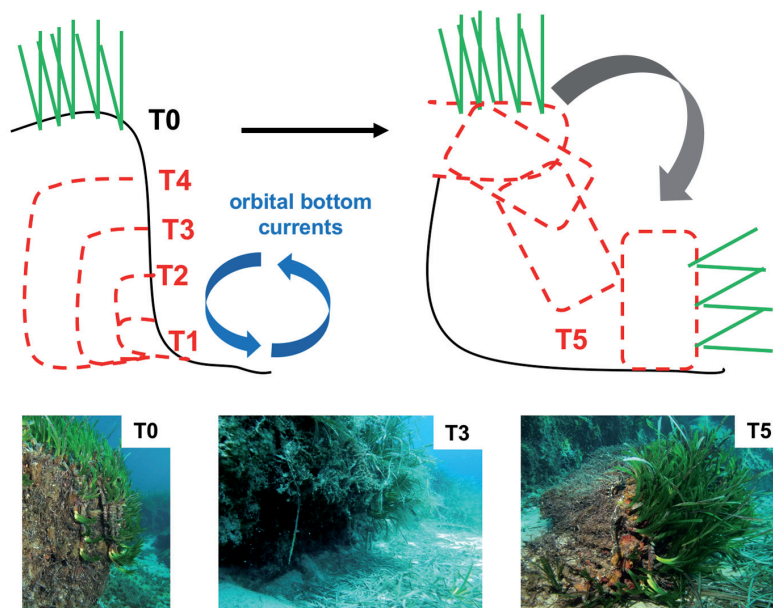

Fig. 6: Temporal evolution of the vertical edge on the eroded side. T0: sheer edge, T1 to T4: erosion of edge bottom, T5: collapsing of the meadow overhang (photos: A. Abadie).

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Finally, due to the parallel and equivalent dynamics of their eroded and colonized sides, the five studied SCs progress simultaneously toward the coastline. Their speed of progression probably depends on the weather conditions (storms, wind direction, and speed, which force the currents) and may also be influenced by the meadow structure (e.g., density, matte compactness on the cliff edge, sediment retention). Considering a mean speed movement of 10 cm.a^{-1} and their landward distance, we predict that the studied SCs will reach the coast within 500 to 600 years.

Conclusion

The spatial dynamics of *P. oceanica* is a process extending over centuries (Meinesz & Lefèvre, 1984; Boudouresque *et al.*, 2009; Vermaat, 2009). However, the exceeding slowness of this process complicates the direct measurement of the progression of sand patches and the seagrass meadow. Nevertheless, this study has shown evidence of recolonization of natural sand patches by *P. oceanica* shoots. We have described, for the first time, the progression of SCs toward the coastline, highlighting an enhanced shoot recruitment and rhizome growth rate on their colonized side. At the opposite regressive side, a high shoot removal rate balances the colonization process, creating vertical edges. These kind of structures have also been observed in other places around Corsica and the Mediterranean Sea, from the upper to the lower limit of the meadow (Borg *et al.*, 2009; Pedersen *et al.*, 2011). The results obtained by using a simple and cost-effective method provided precise data on the spatial evolution of natural patches within the *P. oceanica* seascapes.

Acknowledgements

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