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Assessing *Posidonia oceanica* recolonisation dynamics for effective restoration designs in degraded anchoring sites

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ABSTRACT

The Mediterranean seagrass species *Posidonia oceanica* forms extensive meadows that provide numerous ecological and economic services. Among the human activities threatening these meadows, boat anchoring causes severe degradation resulting in meadow fragmentation, exposure of the dead matte, and sediment disruption. In this study, we assessed the natural recolonisation dynamics of *P. oceanica* in anchoring-degraded sites focusing on both shallow and deep sites. Over two years, photogrammetry was employed to monitor recolonisation dynamics with a focus on patchs' edges expansion and storm-fragments accumulation. Our results show distinct recolonisation patterns between shallow and deep sites, with shallow patches displaying more variable dynamics of erosion and recolonisation, while deep patches showed slower but more consistent recovery. Additionally, the abundance of storm-fragments, primarily in shallow areas, suggests potential for enhanced recovery through natural trapping structures. Despite recent regulations reducing anchoring pressures, recolonisation rates remain insufficient to counteract the extent of degradation in a reasonable timespan. These findings underline the importance of designing tailored restoration strategies based on site-specific recolonisation potential: high-density transplantation with durable anchoring structures in shallow areas to withstand hydrodynamic forces, and more cost-effective solutions like iron staples in deeper areas. Additionally, the study supports the use of trapping substrates to retain storm-fragments in shallow sites to boost natural recolonisation. This approach is crucial for enhancing seagrass meadow resilience, especially within a context of climate change and increasing pressures on coastal ecosystems.

1. Introduction

Posidonia oceanica L. Dellile is a seagrass species endemic to the Mediterranean Sea, where it forms extensive meadows of critical importance due to the wide range of ecosystem services they offer, acting as nurseries (Campagne et al., 2014), serving as carbon sinks (Monnier et al., 2022; Pergent-Martini et al., 2021), and providing protection against coastal erosion (Gacia et al., 1999; Gacia and Duarte, 2001). *P. oceanica* thrives at depths between 0.5 m and 40 m in low turbid waters (Gobert et al., 2006) and is sensitive to strong hydrodynamic conditions, such as wave-induced physical damage and matte erosion (Boudouresque et al., 2006; Ruju et al., 2018). This seagrass species can tolerate temperatures ranging from 9 to 29 °C (Boudouresque and Meinesz, 1982), although this species is sensitive to increases in water temperature and growth is limited above 27 °C (Guerrero-Meseguer et al., 2017; Stipcich et al., 2022a). Besides the rising seawater temperature, global warming also poses significant threats to *P. oceanica* meadows through sea level rise, and the introduction of exotic species leading to the displacement of seagrass communities (Pergent et al., 2014; Stramska and Aniskiewicz, 2019). Moreover, human activities can affect *P. oceanica* meadows (Boudouresque et al., 2009; Giakoumi et al., 2015) both indirectly, by deteriorating water quality (Bockel et al., 2024; Montefalcone et al., 2007), and directly, through habitat destruction caused by coastal development (Holon et al., 2015; Mancini et al., 2023), trawling (Kiparissis et al., 2011), or anchoring (Abadie et al., 2016, 2019; Pergent-Martini et al., 2022). Over half of the world's large (i.e. > 24 m length) recreational boats spend the summer months in Mediterranean waters (Carreño and Lloret, 2021), primarily in the North-Western Mediterranean (Pergent-Martini et al., 2022). Anchoring activities,

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mainly in shallow waters, cause both direct and indirect damage during the process of anchor deployment and retrieval, as well as from the movement of the chain or rope. Repeated anchoring of recreational boats at depths >15 m results in widespread degradation of these meadows (Abadie et al., 2015). The removal of the *P. oceanica* foliar canopy and the belowground organs lead to the exposure of the matte, which consists solely of the remaining rhizomes, roots, and sediment particles: this formation is referred to 'Dead matte'. Beyond the physical damage, this can also cause chemical alterations in the sediment. Initially, carbonate sediments, which may be oxygenated by the presence of living plants, gradually transition to fine particles that fill gaps within decaying organic matter, resulting in an anoxic bare mat (Boudouresque et al., 2016; Mateo and Romero, 1997; Pergent et al., 2014). This change in substrate quality can lead to the infiltration of hydrogen sulphide (H_2S) (Abadie et al., 2016), a chemical compound that inhibits the growth and development of *P. oceanica* (Calleja et al., 2007; Holmer et al., 2003; Marbà et al., 2006). Furthermore, the dead matte left behind by anchoring provides an ideal environment for invasive species like *Caulerpa cylindracea* to establish and spread (Casoli et al., 2021; Katsanevakis et al., 2010; Kiparissis et al., 2011). This macroalga increases hydrogen sulphide concentrations in the sediments, further hindering the potential for *P. oceanica* to recolonize the dead matte (Garcias-Bonet et al., 2008; Holmer et al., 2009).

The implementation of French prefectorial decrees banning anchoring in *P. oceanica* meadows for boats over 45 m in 2016 (Préfecture maritime de Méditerranée, 2016) and for boats over 24 m in 2019 (Préfecture maritime de Méditerranée, 2019) has led to a significant reduction in the degradation of these meadows (Bockel et al., 2023). Once the causes of meadow regression have ceased, natural recolonisation can occur through the expansion of a meadow's edge due to the growth of plagiotropic rhizomes, the dispersal of cuttings by currents (especially during storms) (Boudouresque et al., 2021)., and the recruitment and establishment of seagrass patches via seedlings (Balestri et al., 2017; Boudouresque et al., 2021). However, while the detrimental effects of anthropogenic pressures and declining environmental conditions on seagrass beds are well-documented, the phenomenon of natural recolonisation has received little attention (Almela et al., 2008; Bockel et al., 2024; Kendrick et al., 2005a, 2005b; Olesen et al., 2004). The lack of studies on this topic is particularly concerning given the increasing number of *P. oceanica* meadow restoration projects in recent years (Boudouresque et al., 2021; Pansini et al., 2022). Indeed, the assessment of natural recolonisation following a disturbance is essential when considering seagrass restoration operations (Boudouresque et al., 2021; Cunha et al., 2012). Active restoration is justified only after observing natural recolonisation at the intended restoration site, demonstrating the return of suitable environmental conditions (Boudouresque et al., 2021; Descamp et al., 2025; Mancini et al., 2022; Unsworth et al., 2024). Additionally, comparing transplanted areas with the site's natural recolonisation capacity is crucial for an objective assessment of the restoration efforts' costs and benefits (Boudouresque et al., 2021). In May 2022, a pilot project was launched in the Bay of Calvi (North-Western Corsica, France) to restore *P. oceanica* meadows by transplanting cuttings onto dead matte resulting from anchoring degradation (Boulenger et al., 2024). Alongside these transplantation trials, the natural recolonisation of the *P. oceanica* at the restoration sites is being monitored using photogrammetry, an accurate and low-cost mapping technique (Marre et al., 2020). Specifically, the main objective of this study was to assess the recovery dynamics of *P. oceanica* within degraded areas at shallow and deep sites in North-Western Corsica. Our aims were to assess whether there were differences in recolonization rates between shallow and deep sites and to determine the relative importance of patch recruitment rate in *P. oceanica* spatial colonization by measuring the inter-annual variation in patch size distribution, as well as the accumulation and establishment of drifting vegetative fragments. Additionally, differences in environmental conditions, including temperature and sediment characteristics, that may influence recolonization dynamics at the two study depths, were measured. Finally, the implications of *P. oceanica* recovery dynamics for improving seagrass restoration designs are discussed.

2. Material and methods

2.1. Study area

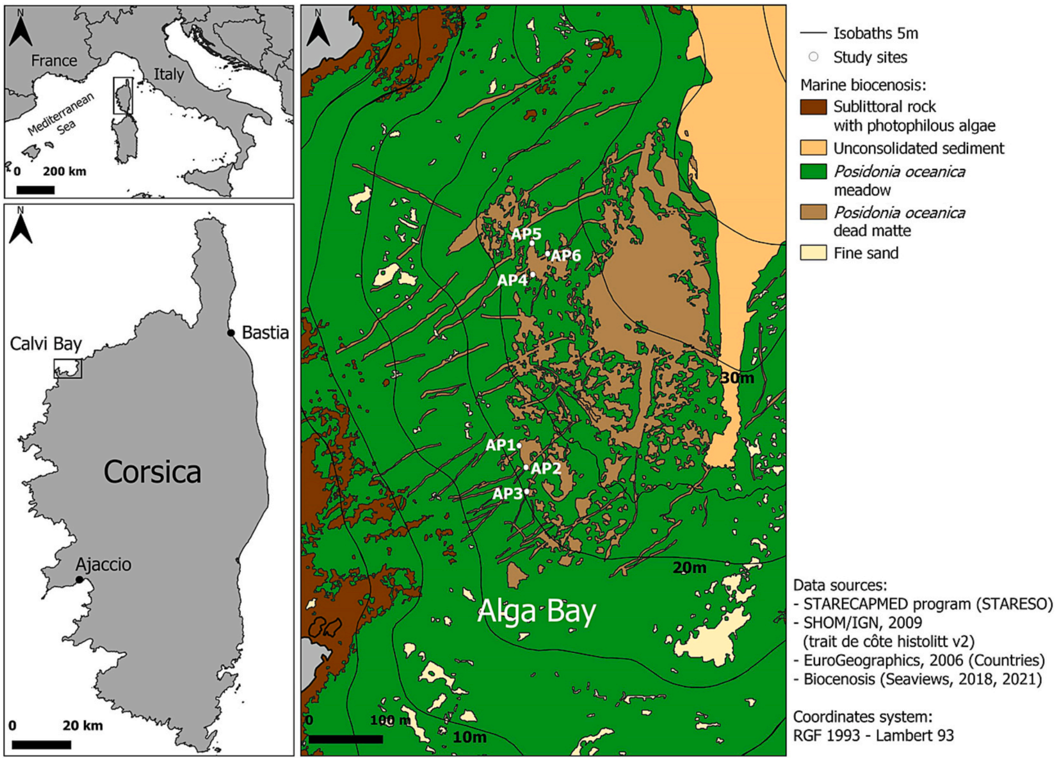
The study sites were located in Alga Bay (8°43′52″ E; 42°34′20″ N), a sub-bay of the Bay of Calvi in North-Western Corsica (France) (Fig. 1). Alga Bay covers a total area of 1 km^2 and features a specific characteristic known as 'return river,' a large sandy area where seagrass meadows are unable to thrive, likely due to bottom currents generated by surface currents reflecting off the coast (Boudouresque and Meinesz, 1982). An extensive *P. oceanica* meadow, covering a total area of 78 ha and located between 3 and 37 m depth, is present in Alga Bay (Fig. 1) (Abadie et al., 2016). This meadow has a good ecological status based on the PREI index (Gobert et al., 2009). The only anthropogenic stressor is the anchoring of leisure boats (Fullgrabe et al., 2022). Indeed, intensive anchoring activity over the last decades has led to severe seagrass meadow loss due to mechanical destruction, with an estimated 8 ha lost in Calvi Bay between 2012 and 2018 (Fullgrabe et al., 2022). Since the enforcement of the new decree in 2019, the proportion of boats over 20 m in length dropping anchors in *P. oceanica* meadows has decreased by 43.8 % (Fig. S1). The bare areas of dead matte are heavily colonized by the invasive macroalga *C. cylindracea* (Fig. 2A), and to a lesser extent by the native macroalga *C. prolifera* (Fig. 2B).

Three patches of dead matte were selected as study sites at two different depths: 20 m (sites AP1, AP2 and AP3) and 28 m (sites AP4, AP5, and AP6) depth, since most of the degradation caused by anchoring pressure occurs in the deeper portion (20-35 m) (Fig. 1). The patches of dead matte selected in this study were chosen because they correspond to restoration sites used in the *REPAIR* project, where *P. oceanica* cuttings were transplanted in spring 2022 (Boulenger et al., 2024). Thus, recolonisation can be compared between natural and transplanted areas, providing a more objective assessment of the effectiveness of the tested restoration techniques (Boudouresque et al., 2021).

2.2. Environmental parameters

Seawater temperature was monitored to determine whether warming affects *P. oceanica* recovery dynamics at shallow and deep sites by influencing the expansion or reduction of seagrass patches' size and the recruitment rates of new seagrass patches. To achieve this, seawater temperature was recorded at the study depths using HOBO loggers (HOBO Pendant Temperature Data Logger, Onset Computer Corporation) at 10-min intervals from May 2022 to May 2024. The loggers were placed just above the dead matte at the six study sites. Due to recording errors by the data loggers, no data were recorded at 28 m for the time intervals from 2022/05/01 to 2022/08/16, and from 2024/03/27 to 2024/04/15. At 20 m, data were missing only for the time interval from 2024/03/27 to 2024/04/15.

Besides seawater temperature, sediment characteristics also play a key role in the spatial colonization dynamics of *P. oceanica*. More specifically, the organic matter buried in the sediment is an important source of nutrient to seagrasses (Evrard et al., 2005; Fraser et al., 2016; Kilminster et al., 2006), and sediment granulometry partly determine porewater nutrient availability (de Boer, 2007; Holmer et al., 2001). Therefore, sediment cores (20 cm depth x 5 cm diameter) were collected in May 2024 to characterize the sediment granulometry and organic matter content of the seafloor at the six study sites. Five samples were taken in the dead matte from each of the six study sites ($n = 30$). In addition, five samples were also collected in nearby *P. oceanica* meadows at both study depths ($n = 10$). After field collection, samples were stored at −20 °C and sent to MicroPolluants Technology SA (Saint Julien Les Metz, France). Sediment cores were dried at 60 °C and passed



Data sources:
- STARECAPMED program (STARESO)
- SHOM/IGN, 2009 (trait de côte histolitt v2)
- EuroGeographics, 2006 (Countries)
- Biocenosis (Seaviews, 2018, 2021)

Coordinates system:
RGF 1993 - Lambert 93

Fig. 1. Location of the study area. The top left figure shows a wider view of Corsica and surrounding countries. The bottom left figure displays a more detailed view of Corsica and the location of Calvi Bay. The figure on the right shows Alga Bay with associated marine biocenosis, the isobaths every 5 m depth and the six study sites (AP1 – AP6).

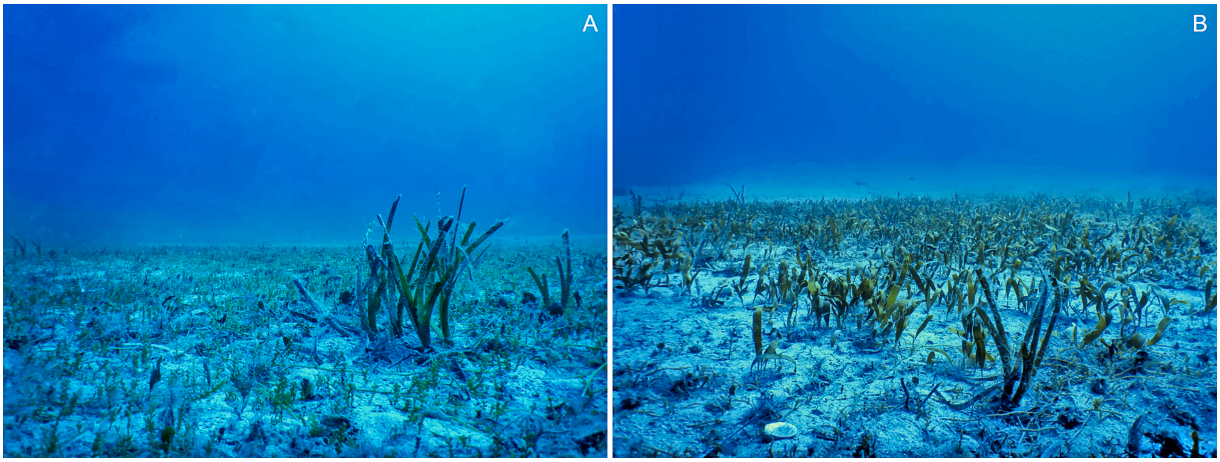


Fig. 2. Thin layer of sand covering the dead matte with a few scattered *P. oceanica* shoots. This area provides a suitable substrate for colonization by two different macroalgae species: (A) a dense network of *C. cylindracea*, (B) a canopy of *C. prolifera* but the presence of *C. cylindracea* in the forefront of the picture can also be noticed. Both photos were taken at 28 m depth in close vicinity to the study site AP6.

through a 2 mm diameter sieve to remove the coarser fraction of the sediment. The percentage of organic matter in each sediment sample was determined by loss on ignition (LOI), combusting at 550 °C for 4 h (Heiri et al., 2001). Inorganic carbon was then removed from the samples by combustion at 950 °C for 2 h (Heiri et al., 2001) before grain size determination. A small amount of sediment from each sample, with organic matter and inorganic carbon removed, was placed in circulating water under continuous sonication for sediment composition analysis (i. e. the percentages of clay, silt, and sand) and median grain size measurements using laser-diffraction (Pratica LA-960, HORIBA Ltd., Kyoto, Japan). Finally, sediment classification was performed according to Wentworth's grain size classes (Wentworth, 1922).

2.3. Monitoring of *P. oceanica* natural recolonisation dynamics by photogrammetry

2.3.1. Underwater images acquisition

To monitor natural recolonisation of *P. oceanica* on dead matte, photographic surveys were conducted at each site ($n = 6$) by a scuba-diver at an average distance of 5 m from the sea bottom conducting parallel, regularly spaced transects. Surveys were carried out at a relatively low swimming speed of 20–25 $m.min^{-1}$, with a time-lapse of approximately 1 s between pictures (photo density: 4–5 photos/m^2) as recommended by Marre et al. (2019). The photographs were taken with a pure nadiral orientation using a 20.1 Mega Pixels Sony Cyber-Shot

RSC-RX100 Va in a waterproof Nauticam housing, with the following settings: shutter speed = automatic, aperture = F12, sensibility = 400 ISO. In some cases, the settings were slightly adjusted depending on environmental conditions (e.g., lighting and visibility) at the time of sampling. Focus was set automatically before each acquisition. The surveys were conducted over two years (2022–2024), each year during the same period (May–June) to avoid differences in leaf growth stages. The total acquisition time per site ranged between 33 and 53 min; with a total of 173 to 701 photos collected per site.

2.3.2. *Photogrammetric images processing*

When necessary, the images were batch-processed for quality improvements using Darktable v4.6.1, enhancing colour contrast, brightness and sharpness. They were then processed with Agisoft Metashape Professional v1.8.4 (Agisoft LLC, 2022), a commercial photogrammetry software extensively used in the scientific community for seagrass meadow monitoring (Abadie et al., 2020; Bockel et al., 2024; Marre et al., 2019, 2020; Piazzolla et al., 2024; Ventura et al., 2022, 2023). This software follows a classic photogrammetric workflow, including images alignment, automatic identification of key points in all photos, bundle adjustment, point cloud densification, mesh building, texturing and orthomosaic production. The specific parameter settings for the different steps of the photogrammetric workflow are provided in Table S1. As the photogrammetric process requires known reference distances to produce metric results, reference makers with known distances between them, called scale bars, were used (Rende et al., 2022; Ventura et al., 2022). Scale bars are particularly useful when it is not feasible to place ground control points across the entire site. They offer a more time-efficient alternative, as placing a few accurately measured scale bars is simpler than using specialized equipment to determine the coordinates of multiple markers (Agisoft LLC, 2022). Six scale bars were installed on the seafloor of each site just before the start of the transects and were used for alignment optimization after bundle adjustment. Scale bars with an error >10 cm were removed from the model. Half of the scale bars ($n = 3$) were not included in the alignment optimization but were retained as validation scale bars to assess the accuracy of internal measurements after bundle adjustment (Ventura et al., 2022). The scale bars placed in the mapped area included four coded markers fixed to a 1 × 1 m cross-scale bar with the same coded marker consistently oriented north using a compass. This configuration ensured that all models were aligned uniformly (Abadie et al., 2022). Moreover, these scale bars were positioned at the same locations each year using rebars placed into the dead matte. This setup allowed the markers on the scale bars to function as fixed reference points, facilitating relative positioning by aligning the orthomosaics of each site over the two years of monitoring (Abadie et al., 2022). All orthomosaics were exported in a TIFF format with a resolution of 0.0003 m to preserve the local metric coordinate system for further GIS analysis.

2.3.3. *P. oceanica natural recolonisation monitoring over time*

To monitor *P. oceanica* natural recolonisation, four monitoring quadrats (3x3m) near the transplantation units were initially randomly selected on the orthomosaics of each study sites ($n = 24$) (Fig. 3). This framing approach allowed for smaller-scale analysis and accelerated data processing. Within each of these 9 m^2 quadrats, the seagrass area (m^2) was manually digitized and quantified using QGIS v3.36.1 (Fig. 3). The seagrass area within each quadrat was measured annually to assess whether there was stability, an increase, or a reduction in the total seagrass area and in the individual surface area of each seagrass patch at the two study depths. Moreover, measuring the inter-annual variations in seagrass area (m^2) allowed us to calculate the annual average recolonization and erosion rates (m^2/year) for each site. The percentage cover of *P. oceanica* in each quadrat was calculated as the ratio of seagrass area (m^2) to the quadrat area (m^2). This metric was used to classify the fragmentation level at each study site. The fragmentation level describes the complex spatial patterns used to analyze landscape configuration (Saura, 2002). Different levels of fragmentation were defined by Sleeman et al. (2005) to characterize seagrass seascapes along a continuum of decreasing patch size and increasing isolation, ranging from large continuous seagrass meadows to many small, dispersed seagrass patches. They are five categories based on the proportion of seagrass cover:: many small patches for seagrass cover below 16 %, medium patches represent 16 %–32 %, few large patches cover 32 %–45 %, fragmented continuous meadows cover 45 %–86 %, and fully continuous meadows exceed 93 % seagrass cover (Sleeman et al., 2005).

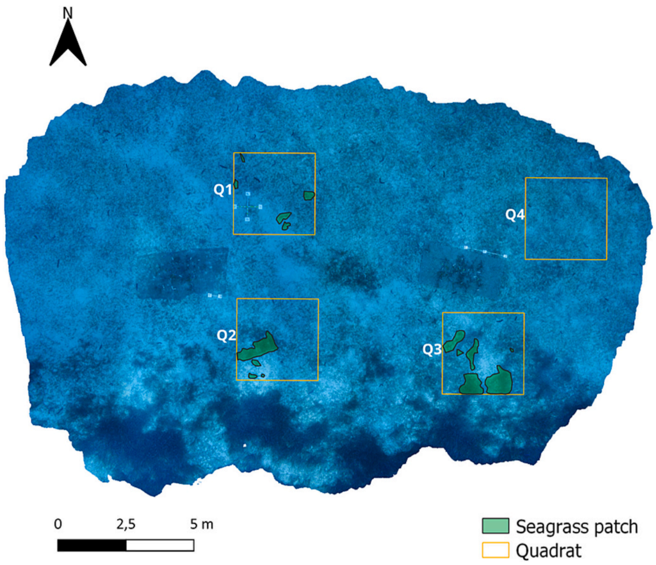


Fig. 3. Orthophoto of one of the study sites (AP4 located at 28 m depth in May 2024) with the manual delineation of *P. oceanica* patches within the four quadrats (Q1 to Q4) placed in a dead matte area. The three transplantation sites of the REPAIR project are also visible on the orthophoto (see Boulenger et al., 2024).

Measuring the inter-annual variations in seagrass area, percent cover, and annual recolonization and erosion rates provided an initial insight into the recovery dynamics of *P. oceanica* at shallow and deep sites. However, to obtain more precise information on recovery dynamics, it is essential to monitor patch population dynamics (Almela et al., 2008). To achieve this, each individual seagrass patch within the monitoring quadrats was assigned to one of ten size classes, with each category defined by a doubling of the previous size (Almela et al., 2008). The temporal evolution of patch size distribution allowed us to determine whether seagrass patches tend to increase in size over time and to assess the recruitment of new seagrass patches. Finally, the number of drifting vegetative fragments (hereafter referred to as storm-fragments) were counted within each quadrat over the two-year monitoring period to assess the potential for new *P. oceanica* patches initiation and recruitment.

2.4. *Data analysis*

Differences in median grain size, mud content and organic matter content were tested using a two-way ANOVA, with Biocenosis (dead matte vs. *P. oceanica* meadow) and Bathymetry (shallow vs. deep) as independent variables to assess how sediment characteristics vary between degraded and vegetated areas and across depths. Prior to the ANOVA test, normality and linearity of the residuals were assessed by visual inspection of residuals versus fitted values plots and with a Shapiro-Wilks test. Levene's test was used to check for homogeneity of variances. Since the normality assumption was not met for mud content and organic matter content, data were log transformed. Differences in *P. oceanica* meadow area, percent cover, number of patches and number of storm-fragments were tested using the non-parametric Kruskal-Wallis test with Time (0, 12, 24 months) and Bathymetry as factors to evaluate temporal trends in *P. oceanica* recolonization and depth-related differences. A non-parametric test was chosen as normality could not be achieved. Statistical significance was set at $p < 0.05$. Statistical analyses were performed in RStudio v4.3.2 (RStudio Inc., Boston, MA, USA). All values are reported as mean ± standard error.

3. Results

3.1. Environmental parameters

The seawater temperature ranged from a maximum of 27.1 °C at 28 m and 26.8 °C at 20 m in September 2022 to a minimum of 13.7 °C at both 28 m and 20 m in February 2023 (Fig. 4). Seasonal variations were pronounced, and thermal stratification was observed in spring 2023 and 2024, with temperatures higher at 20 m than at 28 m. This thermal stratification gradually dissipated as summer approached (Fig. 4).

The median grain size was significantly higher at the shallow sites compared to the deeper sites ($p = 0.015$; $F = 6.765$), while no significant differences were found between the dead matte and *P. oceanica* meadow (Fig. 5). The mud content (0.01 μm < grain size <63 μm) showed the opposite pattern, with significantly higher values for the deeper sites compared to the shallow sites ($p = 0.009$; $F = 8.103$) (Fig. 5). Both Biocenosis and Bathymetry had a significant influence on the organic matter content, with higher values for the deep sites compared to the shallow sites ($p = 0.009$; $F = 7.977$) and higher values in the *P. oceanica* meadow compared to dead matte ($p = 0.003$; $F = 11.100$) (Fig. 5).

3.2. *P. oceanica* meadow recovery dynamics

The six selected patches of dead matte exhibit considerable heterogeneity in area, with no apparent relationship to their depth (Table 1). Their average size is 191.5m^2, with individual patch areas ranging from 56.6m^2 at a depth of 20 m to 319.2m^2 at a depth of 28 m (Table 1).

The two-year monitoring of the area covered by the *P. oceanica* seagrass bed showed high variability within the 24 quadrats across the 6 study sites. The largest seagrass area measured 4.15m^2 in one of the quadrats at site AP3, located at 20 m depth. Conversely, some quadrats exhibited a seagrass area of 0.00 m^2, as observed at site AP4 at 28 m and site AP2 at 20 m. The temporal dynamics of *P. oceanica* meadow area and relative cover over the two years of monitoring showed a slight progressive trend for both shallow and deep sites (Fig. 6). For the shallow sites, the mean colonized seagrass area increased by 12.90 %, from 1.24 ± 0.40 m^2 at the start of the monitoring to 1.40 ± 0.46 m^2 two years later (Fig. 6). A mean progression of 35.13 % was observed for the deep sites, from 0.74 ± 0.17 m^2 at 0 months to 1.00 ± 0.24 m^2 after two years (Fig. 6). In terms of *P. oceanica* meadow percent cover relative to the dead matte cover, there was an increase from 13.82 ± 4.46 % initially to 15.57 ± 5.17 % after two years for the shallow sites (Fig. 6). A similar pattern was observed for the deep sites, with an initial 8.12 ± 1.96 % cover increasing to 11.14 ± 2.66 % two years later (Fig. 6). According to the fragmentation classification by Sleeman et al. (2005), there was a high level of fragmentation, with the meadow primarily consisting of small sized seagrass patches as the percent cover was always lower than 16 % (Fig. 6). No significant differences were found in seagrass area or percent cover between the three monitoring campaigns ($p = 0.860$; $\chi^2 = 0.300$; $p = 0.845$; $\chi^2 = 0.337$; respectively) or between sites at the two different depths ($p = 0.937$; $\chi^2 = 0.006$; $p = 0.915$; $\chi^2 = 0.011$; respectively) (Fig. 6).

The measurement of the inter-annual variations in seagrass area (m^2) allowed us to calculate the annual average recolonization and erosion rates (m^2/year) for each depth (Fig. 7). Both recolonisation and erosion (i.e. regression in seagrass area) processes were observed at each study site, although some sites (i.e., AP3 at 20 m; AP4 and AP5 at 28 m) showed very limited erosion (Table S2). Significant disparities were also observed within the quadrats across the different study sites. For the shallow sites, a maximum recolonisation rate of 0.59 m^2/year and a maximum erosion rate of 0.25 m^2/year were observed (Table S2). For the deep sites, a maximum recolonisation rate of 0.81 m^2/year and a maximum erosion rate of 0.14 m^2/year were recorded (Table S2). The mean annual recolonisation and erosion rates exhibit different patterns depending on the depth (Fig. 7). The deep sites show a higher mean recolonisation rate (0.20 ± 0.06 m^2/year) compared to the mean erosion rate (0.07 ± 0.01 m^2/year) (Fig. 7). In contrast, the shallow sites

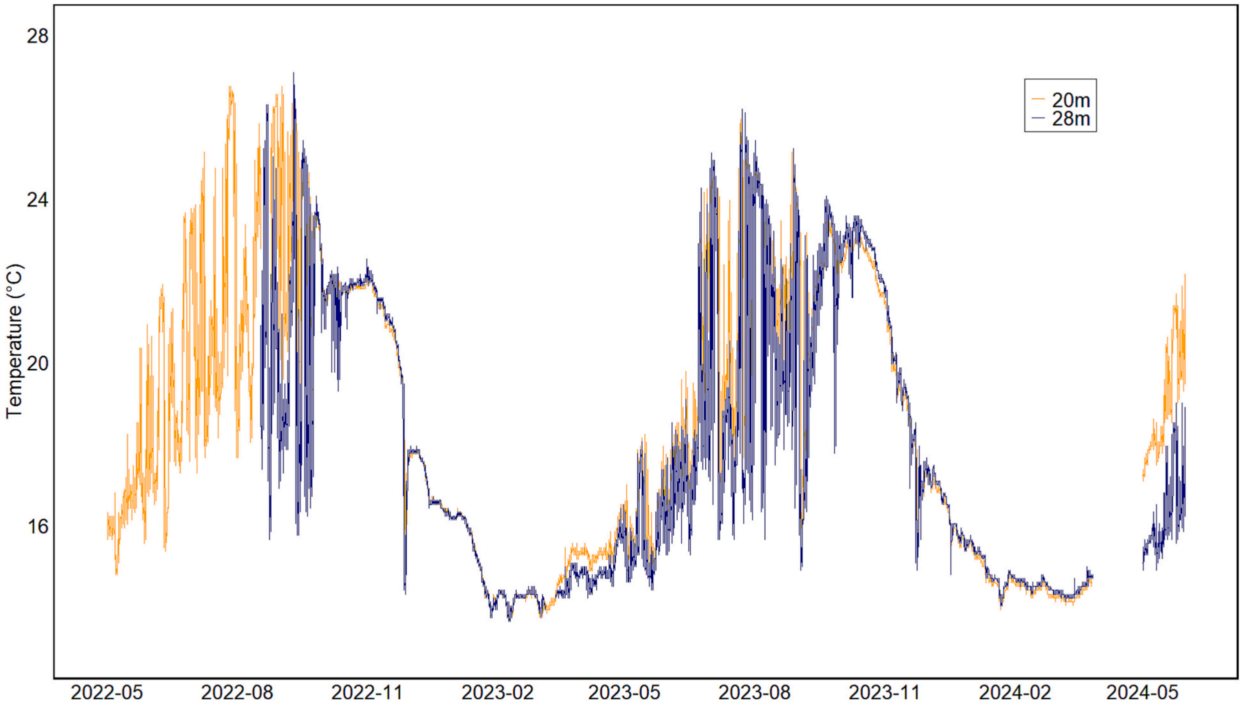


Fig. 4. Temporal dynamics of seawater temperature at the shallow (20 m) and deep (28 m) study sites from May 2022 to May 2024. Missing data were represented as blank spaces in the figure.

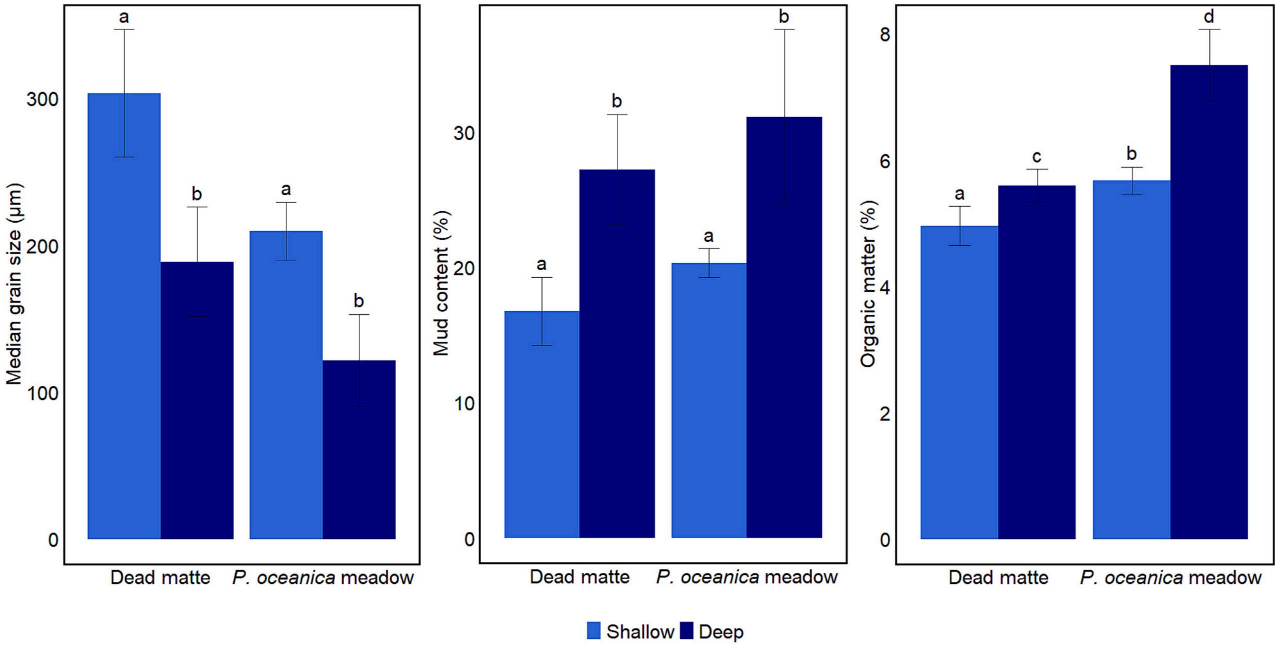


Fig. 5. Mean median grain size (left), mud content (centre), and organic matter content (right) in the dead matte and *P. oceanica* meadow as a function of depth. Vertical error bars represent standard errors. Statistically significant differences are indicated by different letters (a, b, c, and d).

Table 1
Initial dead matte patch area (m^2) at the beginning of the study.

Site	Bathymetry	Dead matte patch area (m^2)
AP1	Shallow	194.2
AP2	Shallow	300.7
AP3	Shallow	56.6
AP4	Deep	226.9
AP5	Deep	319.2
AP6	Deep	206.1

appear to have more balanced processes, with a smaller difference between the mean recolonisation rate (0.16 ± 0.04 m^2/year) and the mean erosion rate (0.09 ± 0.03 m^2/year) compared to the deep sites (Fig. 7). It is also important to note that the mean recolonisation rates are consistently higher than the mean erosion rates regardless of the depth (Fig. 7).

Assessing inter-annual variations in seagrass area, cover, and recolonization/erosion rates offers a first glimpse into *P. oceanica* recovery dynamics. However, precise insights require monitoring patch population dynamics. As it was first observed with the seagrass area, high variability was observed in the number of *P. oceanica* patches within the quadrats. Up to 14 distinct seagrass patches were identified within a single quadrat, while some quadrats contained only one seagrass patch or none at all. No significant differences were observed in the

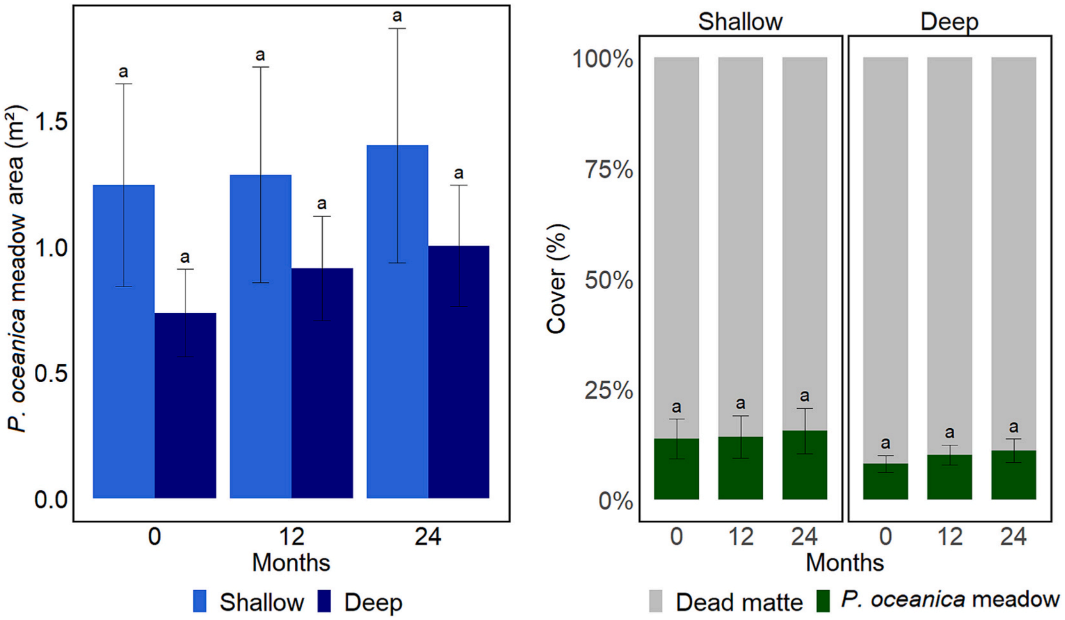


Fig. 6. Mean temporal dynamics of *P. oceanica* meadow area (m^2; left figure) and *P. oceanica* relative cover (%, right figure) as a function of depth. Vertical error bars represent standard errors. The absence of statistically significant differences is indicated by the same letter (a).

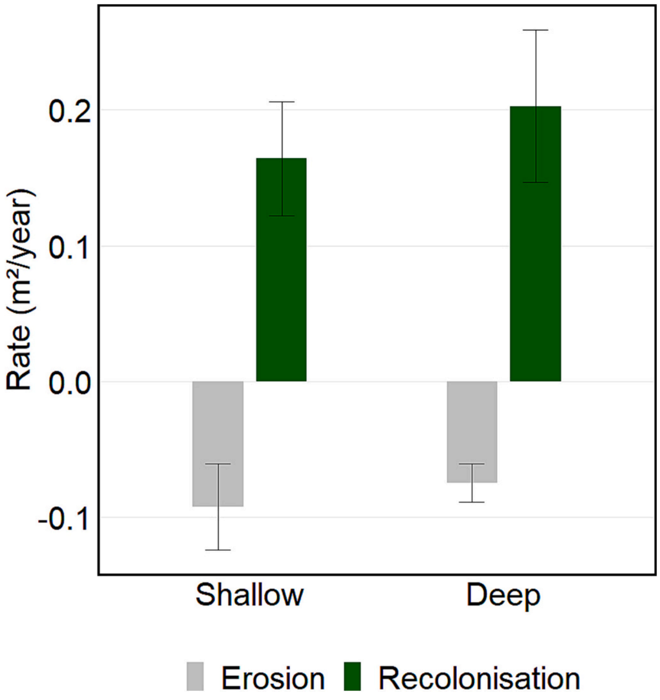


Fig. 7. Mean annual recolonisation and erosion rates (m^2/year) as a function of depth. Vertical error bars represent standard errors. Positive values indicate recolonisation while negative values indicate erosion.

number of seagrass patches over time ($p = 0.089$; $\chi^2 = 4.829$) or between the two study depths ($p = 0.337$; $\chi^2 = 0.921$). The mean number of seagrass patches per quadrats was 4.41 ± 2.75, with a mean size of 0.078 ± 0.027 m^2. In the shallow sites, at the beginning of the study, seagrass patches were primarily distributed across intermediate size classes, notably within the 400–800 cm^2, 800–1600 cm^2, and 1600–3200 cm^2 classes (Fig. 8). After one year, there was a notable increase in the number of seagrass patches within the small and intermediate size classes, as well as an increase in the number of very large seagrass patches (12,800–25,600 cm^2) (Fig. 8). After two years, seagrass patches in the very small size class (0–100 cm^2) disappeared, the number of seagrass patches in the intermediate size classes decreased, and the number of seagrass patches in the 1600–3200 cm^2 class increased (Fig. 8). The number of very large seagrass patches (12,800–25,600 cm^2 and > 25,600 cm^2) remained constant (Fig. 8). For the deep sites, the trend differed. The initial distribution was skewed toward smaller seagrass patches compared to the shallow sites, with a dominance of seagrass patches in the 200–400 cm^2 size class (Fig. 8). After one year, the number of seagrass patches in the 200–400 cm^2 class increased, reaching a peak for this period (Fig. 8). The number of large size class seagrass patches remained lower than in the shallow sites for the same period. After two years, the number of seagrass patches in the small and intermediate size classes decreased, but there was an increase in the number of seagrass patches within certain large size classes (1600–3200 cm^2, 3200–6400 cm^2, and 12,800–25,600 cm^2). However, no very large seagrass patches (>25,600 cm^2) was observed in the deep sites (Fig. 8). Overall, larger seagrass patches were more prevalent in the shallow sites and appeared to persist over time, whereas the deep sites exhibited a dominance of smaller seagrass patches (Fig. 8).

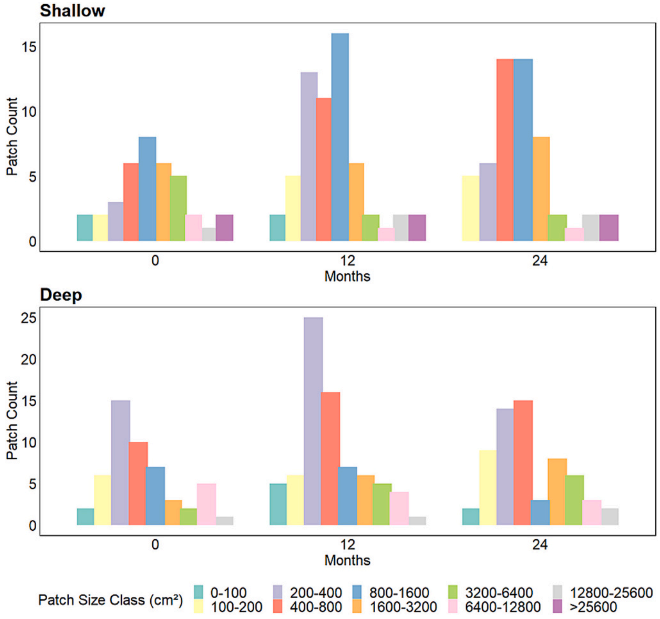


Fig. 8. Dynamics of seagrass patch size distribution (number of seagrass patches within each size class, size as cm^2) over time for shallow (top) and deep (bottom) sites.

Finally, the number of storm-fragments was counted within each quadrat. A large disparity in the quantity of storm-fragments among quadrats at different sites was observed (Table S3). For instance, a maximum of 25 storm-fragments were recorded in 3 % of the quadrats (Table S3), while a substantial portion of the quadrats had no storm-fragments at all (Table S3). No significant difference in the number of storm-fragments between the three monitoring campaigns was observed ($p = 0.371$; $\chi^2 = 1.981$). However, the difference in the number of storm-fragments was significantly related to the depth of the patch of dead matte, with deeper sites experiencing a significantly lower influx of storm-fragments compared to shallower sites ($p = 0.0003$; $\chi^2 = 12.626$) (Fig. 9).

4. Discussion

The establishment of new regulations prohibiting anchoring of large vessels (2016 and 2019), along with an effective reduction in anchoring pressure on the *P. oceanica* meadows and the creation of eco-mooring areas, opens prospects for the ecological restoration of degraded areas. In the past 10 years, there has been a growing number of *P. oceanica* meadow restoration projects throughout the Mediterranean basin (Boudouresque et al., 2021; Pansini et al., 2022), and this trend is set to increase further in the coming years following the adoption of the 'Nature Restoration Law' by the European Parliament in 2024. Most of these restoration projects too rarely evaluate and quantify the dynamics of natural recolonisation at the restored sites (Bockel et al., 2024; Boudouresque et al., 2021). Yet, this data is essential for objectively assessing the cost-benefit ratio of a restoration project compared to natural recolonisation at the study site (Boudouresque et al., 2021).

The natural recolonisation from meadow edges or isolated clumps of *P. oceanica*, as well as the establishment of new patches by storm-fragments, was quite limited in the dead matte areas in this study, which also served as transplantation sites (see Boulenger et al., 2024). Seawater temperature was measured at both shallow and deep sites, as rhizome biomass and length, playing a crucial role in recolonization capacity and speed, are negatively affected by marine heatwaves (MHV) (Pansini et al., 2021; Stipcich et al., 2022b). However, the high temperatures recorded during the summer 2022 MHW (Guinaldo et al., 2023; Marullo et al., 2023) were similar at 20 m and 28 m depths, suggesting a reduced thermal gradient that may drive differences in *P. oceanica* resilience and recolonization potential between both depths. The depth of the patches of dead matte also showed no significant difference in recolonized area or cover after two years of monitoring, which aligns with findings from other studies that measured natural recolonisation on dead matte at various depths (Abadie et al., 2019; Badalamenti et al., 2011). However, a progressive positive trend in seagrass area is

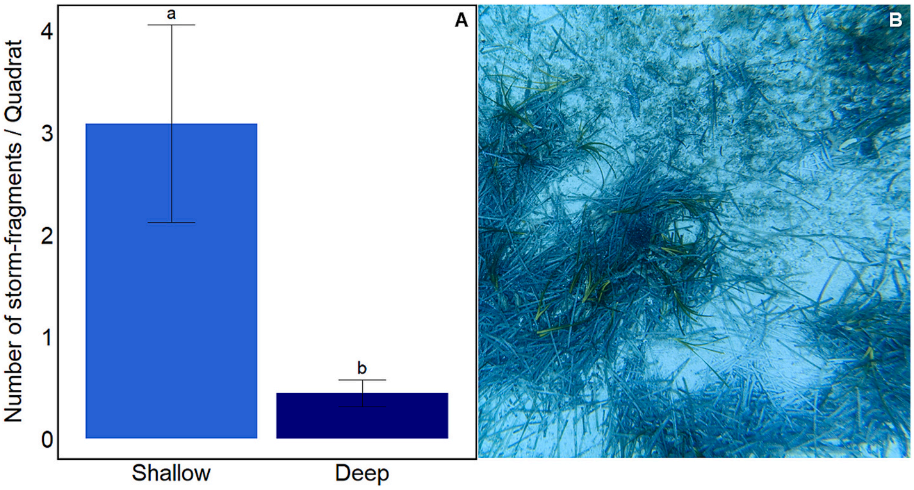


Fig. 9. (A) Mean number of storm-fragments accumulation per 9 m^2 quadrat as a function of depth. Vertical error bars represent standard errors. The statistically significant difference is indicated by different letters (a and b). (B) Important accumulation of storm-fragments on the site AP3 at 20 m depth.

observed for both the shallower sites (35.13 % mean progression) and deeper sites (12.90 % mean progression). These values are consistent with other recent works conducted in the French Mediterranean, such as the 8–46 % progression measured by Marre et al. (2020) or the 5–9.3 % progression measured by Bockel et al. (2024). There appears to be an alternation between erosion and recolonisation processes, with erosion being more prominent at shallow sites compared to deep sites, likely due to the reduction in hydrodynamic forces with increasing depth (Vacchi et al., 2017; Uhrin and Turner, 2018). However, colonization remains the dominant process over erosion for both shallow and deep sites, as observed in other studies (Abadie et al., 2019; Bonamano et al., 2021; Marre et al., 2020).

The favorable recolonisation dynamics demonstrate the remarkable resilience of *P. oceanica* exposed to an altered dead matte, with changes in the below-ground chemical processes (Abadie et al., 2016) and microbial communities (Frasca et al., 2024). The analysis of grain size and organic matter content in the anchoring patches monitored in this study showed few differences compared to the adjacent *P. oceanica* meadows. No significant differences were found between shallow and deep dead matte patches. The range of values observed for both median grain size and mud content corresponds to other measurements on matte characterization in the north-western Mediterranean (Serrano et al., 2012). Only the organic matter content differed, with lower organic matter content in the shallow sites compared to the deeps sites, for both *P. oceanica* meadow and dead matte. The lower organic matter content in shallow sites compared to deep sites is primarily driven by increased hydrodynamic activity (Vacchi et al., 2017; Uhrin and Turner, 2018) and temperature-induced organic matter remineralization (Roca et al., 2022; Trevathan-Tackett et al., 2017) has shown by the strong thermal stratification in spring between shallow and deep sites. Moreover, the organic matter content was also significantly higher in the *P. oceanica* meadow compared to the dead matte. *P. oceanica* meadows are known to sequester a significant portion of their primary production within the underlying matte (Boudouresque et al., 2016), making them a substantial reservoir of organic matter due to the recalcitrant nature of *P. oceanica* necromass (Boudouresque et al., 2016; Mateo et al., 1997; Kaal et al., 2018). The decrease in organic matter content within the dead matte is typically linked to erosion after the loss of the canopy, which leads to increased mineralization of previously buried organic material under newly oxygenated conditions (Marbà et al., 2015; Moksnes et al., 2021; Salinas et al., 2020). It has also been shown that the colonization of dead matte by macroalgae of the genus *Caulerpa* can help preserve sequestered carbon and limit matte erosion by stabilizing the surface layers with their rhizoids (Apostolaki et al., 2022). Additionally, *Caulerpa* species also significantly enrich the sediment with organic carbon through their metabolic production and their ability to trap allochthonous particles (Hendriks et al., 2010; Holmer et al., 2009). However, despite the significant presence of a dense network of *C. cylindracea* (Fig. 2A) and, to a lesser extent, patches of *C. prolifera* (Fig. 2B) at the study sites, this does not appear to be sufficient to maintain the original organic matter content in the dead matte as observed in the surrounding *P. oceanica* meadows. It is likely that most of the matte erosion occurs in winter, as both *C. cylindracea* and *C. prolifera* exhibit marked seasonality in leaf area and have a weak rhizoidal structure, leaving the dead matte unprotected during winter storms (Casoli et al., 2021; Hendriks et al., 2010). Nevertheless, the recolonisation rate measured in this study remains far smaller compared to the rates of several m^2 (Marre et al., 2020), hundreds of m^2 (Pergent-Martini et al., 2002), or even thousands of m^2 per year (Boudouresque et al., 2021) reported by some authors. The extreme values presented in the two latter studies both refer to the recolonisation of dead matte at the lower depth limit resulting from poor water quality and increased water turbidity (Boudouresque et al., 2021), a threat that disappeared following the installation of waste-water treatment plants, which restored appropriate environmental conditions (Bockel et al., 2024; Boudouresque et al., 2021; Pergent-Martini et al., 2002). The direct mechanical action of anchoring, as well as trawling, by tearing out plant shoots or sections of the matte, reducing the meadow cover and increasing meadow fragmentation, led to prolonged effects over time and a very slow rate of recolonisation (Abadie et al., 2016, 2019; González-Correa et al., 2005; Kiparissis et al., 2011).

Besides the alteration in the physico-chemical characteristics of the seafloor, the highly fragmented *P. oceanica* meadows, consisting of numerous small patches with low percent cover (<16 %), struggle to recover also due to isolation and reduced connectivity between patches. Indeed, the average seagrass patch size across the study sites is small (0.078m^2) which also explain the low recolonisation rates measured in this study. The observed high variability in patch number within quadrats, ranging from 1 to 14 patches, further highlights the fragmented nature of these meadows. Seagrass meadows rely heavily on self-facilitation processes, such as an increase in the density of conspecifics, to enhance survival and promote patch expansion (Almela et al., 2008; González-Correa et al., 2005; Valdez et al., 2020; Vidondo et al., 1997). A fragmented seagrass meadow composed of numerous small patches will initially undergo a period of slow vegetative growth in random directions (Kendrick et al., 2005a, b). In our study, we observed an initial period where small and intermediate-sized patches increased in number in shallow sites, particularly within the 400–800 cm^2, 800–1600 cm^2, and 1600–3200 cm^2 classes. However, after two years, very small patches (0–100 cm^2) disappeared, while intermediate-sized patches decreased, and larger patches (1600–3200 cm^2) became more dominant, suggesting a gradual coalescence process. With an increase in shoot density and cover, the patches will coalesce into larger units, thus forming a more continuous meadow with a greater spreading rate (González-Correa et al., 2005; Kendrick et al., 2005a, b). is process was particularly evident in shallow sites, where a few patches reached very large sizes (12,800–25,600 cm^2). In contrast, deep sites exhibited a different trend, with an initial dominance of smaller patches (200–400 cm^2) and a slower transition toward larger patches. Notably, no patches larger than 25,600 cm^2 were observed at deep sites. Large patches can change local hydrodynamics and create shelter in their surroundings, enhancing the survival of nearby small patches. Additionally, they may produce a greater number of vegetative fragments, boosting the recruitment rate of nearby patches (Almela et al., 2008). The recolonisation process in the deep sites occurs almost exclusively through the progression of patch edges, but many storm-fragments were observed in the shallower sites. These fragments could serve as a source for the establishment of new patches, potentially accelerating long-term recolonisation. This hypothesis was also proposed by Pergent-Martini et al. (2022) to explain the high recolonisation rates observed in their study. Meinesz and Lefèvre (1984) determined that the establishment frequency of storm fragments is 3/ha/year, which represents a minimal contribution to recolonisation compared to meadows margins progression, even when considering the low recolonisation rates measured in our study. Indeed, most storm-fragments lack roots, and the dead matte offers little structural complexity to allow these fragments to be trapped, remain stable in one place and develop (Badalamenti et al., 2011). However, studies on natural recolonisation on calcareous rubbles show a significant contribution of storm-fragments to natural recolonisation, as the crevices between adjacent rubbles offer a pattern of substrate complexity enabling the trapping and persistence of *P. oceanica* vegetative fragments (Almela et al., 2008; Badalamenti et al., 2011; Di Carlo et al., 2005). Regarding sexual recruitment through seed germination and seedling establishment, it predominantly occurs in sheltered areas, at shallower depths than the study sites and more frequently on rocky substrate than dead matte (Balestri et al., 2017; Balestri and Lardicci, 2008; Piazzi et al., 1999).

4.1. Implications for restoration

The overall level of fragmentation in the meadow is a key factor in determining the vulnerability of seagrass meadows (Barcelona et al., 2021). Due to climate change, the increasing frequency and severity of storms (Masson-Delmotte et al., 2019) will impact the integrity of *P. oceanica* meadows, especially fragmented meadows in exposed locations (Marco-Méndez et al., 2024). Additionally, climate-induced rises in sea temperature and sea level, which affect light availability, also threaten the resilience of seagrass meadows at upper and lower depth limits (Pergent et al., 2014). Given the very slow natural recolonization observed in our study, it is crucial to emphasize the fundamental importance of protecting *P. oceanica* meadows from anthropogenic activities to prevent further degradation. Moreover, conservation measures and new regulations must be implemented across the entire Mediterranean basin to prevent the displacement of anchoring-related degradation between countries with differing protection laws. Furthermore, active restoration through the transplantation of cuttings (e.g. Boulenger et al., 2024; Mancini et al., 2022) or seedlings (e.g. Mancini et al., 2024; Zenone et al., 2025) can serve as a valuable tool to reduce fragmentation and facilitate the recovery of highly fragmented seagrass meadows, ensuring their resilience in a changing climate. Restoring *P. oceanica* meadows also helps limit the degradation of the dead matte and the mineralization of organic matter, thereby preserving the integrity of the dead matte—a factor that is particularly important for climate change mitigation (Pergent-Martini et al., 2021). Our study highlights the differing recolonisation dynamics between shallow and deep dead matte patches. The insights gained can inform the design of effective restoration plans tailored to local conditions, which we stress as essential for any restoration project. Given the fluctuations between recolonisation and erosion processes at shallow sites, we suggest that transplantation of cuttings should use anchoring structures with a certain level of resistance to local hydrodynamics (Heide et al., 2021; Temmink et al., 2020). Additionally, transplantation should be carried out at high density in relatively large planting units to benefit from the mutual sheltering effect (Valdez et al., 2020; van Katwijk et al., 2016). Considering the relatively high accumulation of storm-fragments in shallow areas, it would also be beneficial to use structures that facilitate their trapping, such as gabions with ten-centimeter gaps between rocks (Badalamenti et al., 2011; Di Carlo et al., 2005). This approach could support natural recolonisation without the need for transplantation or serve as a complementary strategy. A different restoration design should be applied for deeper sites. The limited erosion rate compared to the recolonisation rate suggests that the type of anchoring structures used for transplanted cuttings will have little impact, making more cost-effective solutions, such as the use of iron staples (Mancini et al., 2021), a suitable alternative. The very low quantity of storm fragments in deep sites suggests that using trapping substrates to promote their retention and establishment would be ineffective.

5. Conclusion

This study assessed the recovery dynamics of *P. oceanica* in areas damaged by anchoring at shallow and deep sites in North-Western Corsica. The findings highlight clear differences in recolonisation patterns between shallow and deep sites. Shallow patches of dead matte exhibited more dynamic processes, with alternating erosion and recolonization, while deeper patches of dead matte showed slower yet steadier recovery. The high presence of storm-fragments in shallow areas suggests their potential in aiding recovery by establishing new seagrass patches. However, despite these dynamics, recolonisation remained limited, likely due to alterations in the dead matte's physico-chemical characteristics, such as reduced organic matter content compared to adjacent meadows. This underscores the inherent challenges in the natural recovery of *P. oceanica* meadows and the importance of protecting those meadows against anthropogenic pressures to prevent further degradation. For seagrass meadows that are already heavily damaged and fragmented, ecological restoration offers a viable solution to facilitate the recovery of degraded areas. The findings stress the importance of incorporating site-specific factors into restoration efforts. At shallow sites, where erosion and fragment accumulation are more pronounced, restoration designs could incorporate structures that facilitate fragment trapping and offer stability against hydrodynamic forces. In contrast, deeper sites, characterized by less erosion and very little storm-fragments accumulation, may benefit from simpler and more cost-effective approaches like the use of iron staples for cuttings' transplantation. Across all depths, ensuring the connectivity between seagrass patches and promoting self-facilitation processes will be critical to accelerate recovery. This research underscores the need to assess and monitor natural recolonisation processes before implementing active restoration measures. By aligning restoration strategies with the specific environmental conditions and recolonisation capacities of degraded areas, it is possible to improve restoration success and long-term resilience of *P. oceanica* meadows.

CRediT authorship contribution statement

Arnaud Boulenger: Visualization, Validation, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization, Writing – original draft. **Juliana Chapeyroux:** Methodology, Investigation, Formal analysis, Data curation, Writing – original draft. **Lovina Fullgrabe:** Visualization, Formal analysis, Data curation, Writing – review & editing. **Michel Marengo:** Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization, Writing – review & editing. **Sylvie Gobert:** Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2025.117960.

Data availability

Data will be made available on request.

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