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Comparative assessment of transplantation methods and donor sources for the restoration of *Posidonia oceanica* meadows

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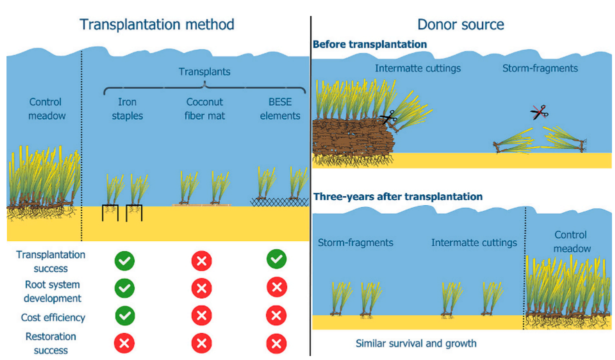
HIGHLIGHTS

- First test comparing storm fragments vs donor cuttings for *P. oceanica* restoration
- Three sustainable methods tested: iron staples, coconut mats, and BESE elements
- Iron staples yield best survival, root growth, and cost-efficiency overall.
- Storm-fragments perform as well as donor meadow cuttings for transplantation.
- Traits still differed from natural meadows after 3 years, indicating partial recovery

GRAPHICAL ABSTRACT



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ABSTRACT

The restoration of coastal ecosystems, especially seagrass meadows, has become a key priority to support the recovery of ecosystem services. In the Mediterranean Basin, although many projects have been carried out to restore *Posidonia oceanica* meadows over the past 50 years, major knowledge gaps persist. This study is the first to simultaneously compare two donor sources, storm fragments versus donor meadow cuttings, and three sustainable transplantation methods. This three-year experiment involved transplanting 693 cuttings using three distinct transplantation methods (iron staples, coconut fiber mats, and BESE elements) in shallow (20 m) and deep (28 m) dead matte areas of Calvi Bay (Corsica, NW Mediterranean). Performance was assessed through survival, shoot production, leaf and root morphological traits, with particular attention given to root systems development, a critical but often overlooked component in seagrass restoration studies. Storm-fragments performed comparably to donor meadow cuttings, supporting their use as a sustainable, non-destructive source of planting material. Among transplantation methods, iron staples led to the best performance across survival, root development, and cost-efficiency. BESE elements ensured high survival but limited root development, while coconut fiber mats performed poorly overall. Despite encouraging survival rates (>80 % under optimal conditions), significant differences in leaf and root traits remained between transplants and natural meadows after 36 months, suggesting incomplete ecological recovery. This comparative approach provides a critical first

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benchmark for evaluating the feasibility, performance, and economic viability of different restoration techniques in *P. oceanica* meadows.

1. Introduction

In February 2024, the European (EU) Parliament adopted the *Nature Restoration Law*. Under this legislation, EU member states are required to restore at least 30 % of terrestrial and marine habitats in poor condition by 2030, 60 % by 2040, and 90 % by 2050. Over the past centuries, many human activities, such as land reclamation, coastal development and water pollution, have significantly contributed to the degradation of European coastal habitats (Airoldi and Beck, 2007). This is especially true for the extensive seagrass meadows formed by *Posidonia oceanica* (L.) Delile, which have experienced a well-documented regression throughout the entire Mediterranean basin (Boudouresque et al., 2009;). These meadows, growing from the surface down to an average 40 m depth, are of considerable ecological and economical importance because of the multitude of ecosystem services they provide such as nursery, carbon sink) and protection against coastal erosion (; (Campagne et al., 2014). *P. oceanica* meadows are impacted by anthropogenic pressures (Boudouresque et al., 2009) either indirectly through degradation of water quality (Bockel et al., 2024) or directly through habitat destruction, such as coastal development (Holon et al., 2015), trawling (Kiparissis et al., 2011) or anchoring (Abadie et al., 2016). Land-based pollution is one of the major anthropogenic threats to coastal ecosystems (Holon et al., 2015). Wastewater discharges contribute to eutrophication by increasing nutrient and organic matter loads, which reduce water clarity, stimulate algal blooms, and cause sediment accumulation. These processes limit light penetration and ultimately compromise seagrass growth and survival. Since 1991, the European Urban Wastewater Treatment Directive (91/271/CEE) has established water quality standards to safeguard receiving ecosystems and required member states to implement action plans to achieve these targets. This directive has since led to substantial improvements in wastewater collection and treatment infrastructure in France, reducing untreated discharges and benefiting *P. oceanica* meadows, particularly at their lower depth limits (Bockel et al., 2024; Boudouresque et al., 2021). Moreover, mechanical damage from anchoring by large recreational boats (hull length > 24 m) (Abadie et al., 2016; Pergent-Martini et al., 2022) is of growing concern due to the increasing popularity of recreational boating in recent decades (Carreño and Lloret, 2021). Anchoring in *P. oceanica* meadows causes both direct and indirect harm through the deployment and retrieval of anchors and the dragging of chains and ropes along the seabed. Repeated anchoring ultimately leads to widespread degradation of the meadows (Abadie et al., 2015; Pergent-Martini et al., 2022). Although the Mediterranean Sea represents less than 1 % of the global ocean surface, it receives more than half of the world's fleet of large recreational vessels, especially during the summer months (Carreño and Lloret, 2021). This activity is predominantly concentrated in the northwestern Mediterranean basin (Pergent-Martini et al., 2022).

In mainland France and Corsica, *P. oceanica* meadows are the marine habitat most impacted by anchoring pressure (Deter et al., 2017). In 2016, French authorities implemented a regulation relative to the anchoring of the largest vessels (>80 m) (French Naval Prefecture, Decree No. 155/ 2016), reinforced by a new regulation in 2019 prohibiting any anchoring within seagrass meadows for boats longer than 24 m (French Naval Prefecture, Decree No. 123/2019). Although a reduction in large boat anchoring in *P. oceanica* meadows has been observed following the enforcement of these regulations (Bockel et al., 2023), the slow growth rate of *P. oceanica* rhizomes (a few centimetres per year) means that natural recolonization of damaged areas is a process that will takes decades or even centuries (Boulenger et al., 2025a). To accelerate the recovery of degraded *P. oceanica* meadows and their associated ecosystem services, active restoration measures such as the transplantation of cuttings have been implemented in areas where the source of degradation has been removed or mitigated (Boudouresque et al., 2021). A wide range of anchoring or stabilization techniques have been employed for *P. oceanica* transplantation, including heavy structures such as concrete frames (Bacci et al., 2024), as well as lighter alternatives using metallic, plastic, or biodegradable meshes and wires (De Luca et al., 2025; Piazzi et al., 2021), or cost-effective devices like stakes and staples (Castejón-Silvo and Terrados, 2021; Mancini et al., 2021). Both grid-based systems (plastic, wire, or natural fibers) and individual anchoring methods (metallic or biodegradable staples and pegs) have generally produced good transplantation outcomes (Calvo et al., 2021; Genot et al., 1994; Mancini et al., 2021; Molenaar and Meinesz, 1995; Piazzi et al., 2021), with some techniques proving effective over the long term. Despite increasing experimental trials of *P. oceanica* transplantation over the past decade, significant knowledge gaps remain (Boudouresque et al., 2021; Pansini et al., 2022; Pergent-Martini et al., 2024). These include the need to test different sustainable anchoring methods to attach the cuttings to the seafloor, as well as different donor sources of plant material for transplantation, across a variety of environmental conditions (Boudouresque et al., 2021; Pansini et al., 2022; Pergent-Martini et al., 2024). This study aimed to address these gaps by: (1) Testing biodegradable substrates of varying structural complexity to facilitate transplants' anchoring; (2) Comparing the performance of transplants from two donor sources: fragments of *P. oceanica* rhizomes either harvested from natural meadows and fragments of unknown origin that are found drifting on the seafloor; and (3) transplanting at two different depths (20 and 28 m), corresponding to the bathymetric zones where significant degradation due to anchoring (Abadie et al., 2015) and wastewater discharge (Bockel et al., 2024) is often found.

2. Material and methods

2.1. Study area

This study was conducted in the sub-bay Alga Bay (8°43′52″E; 42°34′20″N), located within Calvi Bay in northwestern Corsica in the northwestern Mediterranean basin. Alga Bay, situated nearby the STARESO research station, covers an area of 1 km^2 and is colonized by a *P. oceanica* meadow that spans 0.78 km^2 of the seafloor (Abadie et al., 2016) (Fig. 1). Prior to the enforcement of the Decree No. 123/2019, this bay experienced several decades of intensive anchoring activity, which resulted in many anchoring scars within the seagrass meadows, corresponding to the abrasion caused by anchor removal. However, since the implementation of the new regulation, anchoring by leisure boats (>20 m long) in *P. oceanica* meadows has decreased by 57 % in Calvi Bay between 2019 and 2023. The selection of experimental sites followed the decision-making strategy for transplanting *P. oceanica* and other seagrasses proposed by Boudouresque et al. (2021). Seven patches of dead matte, resulting from previous anchoring damage, were selected as experimental sites (Fig. 1). Three sites were located at an average depth of 20 m (AP1 – AP3, hereafter referred to as "shallow" sites) and four at an average depth of 28 m (AP4 – AP7, hereafter referred to as "deep" sites).

2.2. Seagrass transplantation

2.2.1. Transplantation methods

The attachment of cuttings to the seabed is a critical step for the success of seagrass transplantation. Although several methods have been tested in previous studies and proven to be effective, only a subset are considered environmentally sustainable (Boudouresque et al., 2021). In this study, three different biodegradable anchoring methods were tested with the aim of ultimately leaving only the natural ecosystem once the transplants have developed a sufficiently robust root system. The first method used U-shaped iron staples (Fig. 2A), which offered the least protection against hydrodynamic forces. Each staple consisted of a 10 cm straight horizontal section and two 30 cm vertical arms designed to be inserted into the dead matte. Each staple had a thickness of 3 mm. The second anchoring method, commonly used in terrestrial ecological engineering (e.g., for riverbank or dune restoration) (Piazzi et al., 2021), employed a biodegradable mat made of natural coconut fiber, woven into an H2M5 mesh weighing 740 g/m^2 (Ecobiotex, Thizy Les Bourgs, France) (Fig. 2B). The mesh size was 9 × 9 mm, and the mat had a thickness of 5 mm. The third method used BESE elements (BESE Ecosystem Restoration Products, Culemborg, The Netherlands), composed of biodegradable potato-waste-derived Solanyl C1104M (Rodenburg Biopolymers, Oosterhout, the Netherlands) (Fig. 2C). This Solanyl biopolymer is officially certified as biodegradable (see Appendix 1), and it gradually degrades under field conditions over 5 to 10 years, depending on the local environmental conditions. Individual sheets (91.0 × 45.5 × 2.0 cm; 0.44 kg, surface-to-volume ratio 80 m^2/m^3) can be stacked together to form a modular 3D-structure (Fig. 2C). In this study, three sheets were combined to form a 6-cm high 3D honeycomb-shaped matrix allowing for the expansion of seagrass rhizomes and roots through the structure.

The coconut fiber mats and the BESE elements offer greater structural complexity than the staples. Therefore, we hypothesized that they could facilitate transplant anchoring and enhance natural recruitment by trapping drifting fragments and/or seedlings (Fig. 3). These methods draw inspiration from the ecological succession theory, wherein pioneer species create a network of roots and rhizomes that capture drifting cuttings and promote their attachment to the substrate (Fig. S1).

2.2.2. *Experimental design and field transplantation*

A major limitation in *P. oceanica* restoration efforts is the limited availability of planting material, which poses a significant obstacle to large-scale meadow restoration initiatives. To minimize the impact on existing meadows, the use of naturally detached fragments from *P. oceanica* meadows offers a promising, non-destructive alternative to harvesting cuttings directly from donor meadows (Balestri et al., 2011) (Fig. 3A). Indeed, large quantities of seagrass fragments (hereafter referred to as storm-fragments) of various morphologies are naturally uprooted during storms events. There is evidence that *P. oceanica* storm-fragments can colonize new habitats, form new patches, and expand clonally over time (Almela et al., 2008). However, little is known about the performance of those storm-fragments drifting on the seafloor, in terms of survival and growth, compared to the use of cuttings directly extracted from natural meadows (Balestri et al., 2011; Boulenger et al., 2024). Since this comparison is essential for developing ecologically sustainable restoration strategies, both types of cuttings were included in this study (Fig. 3). The majority of the cuttings (462 fragments)

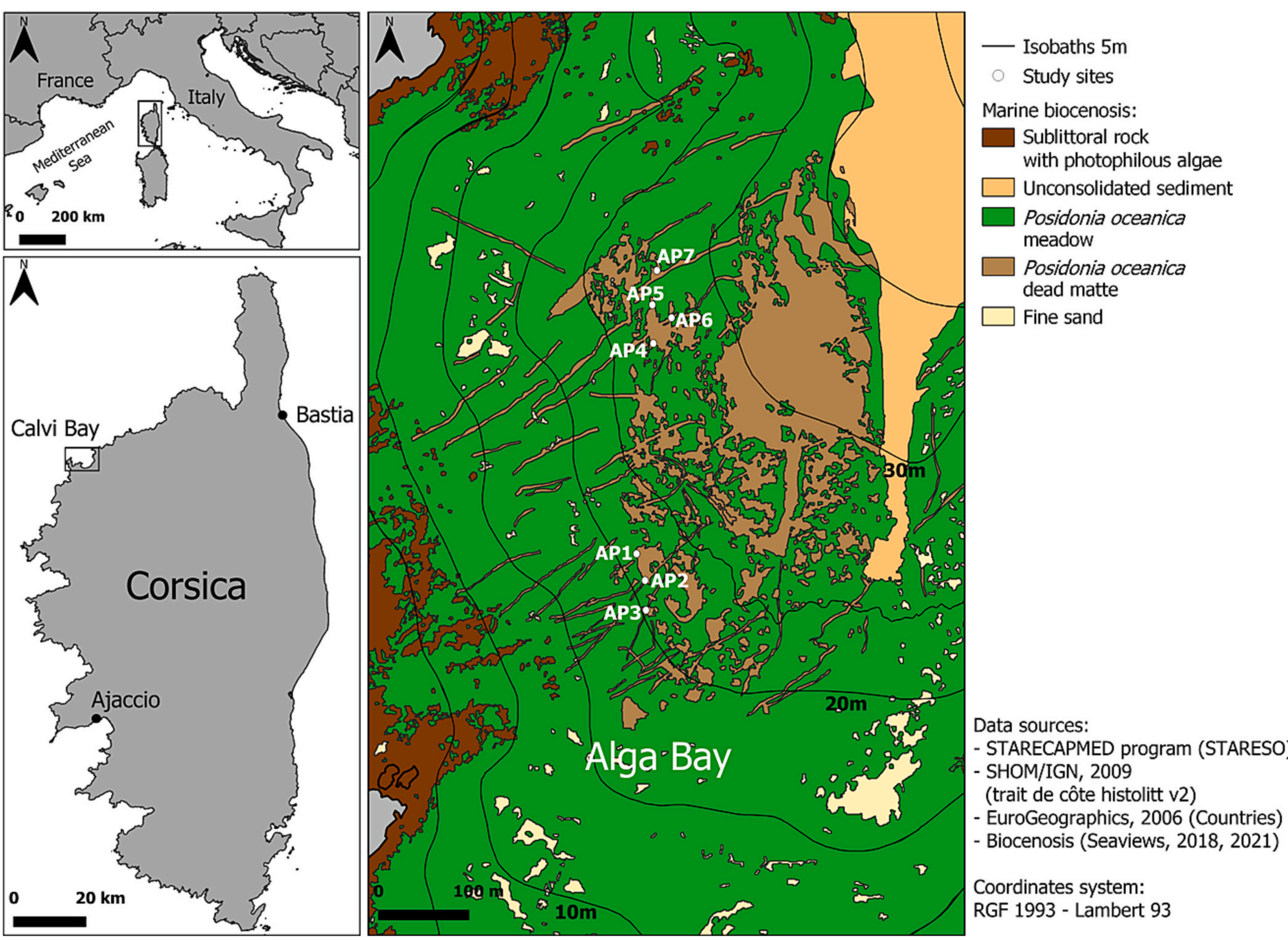

Fig. 1. Location of the study area. The top left figure shows a wider view of Corsica Island in the Mediterranean Sea. The bottom left figure displays a more detailed view of Corsica and the location of Calvi Bay. The figure on the right shows Alga Bay with associated marine biocenosis, the isobaths every 5 m depth and the transplantation sites (AP1 – AP7). Figure modified from Boulenger et al., 2025a.

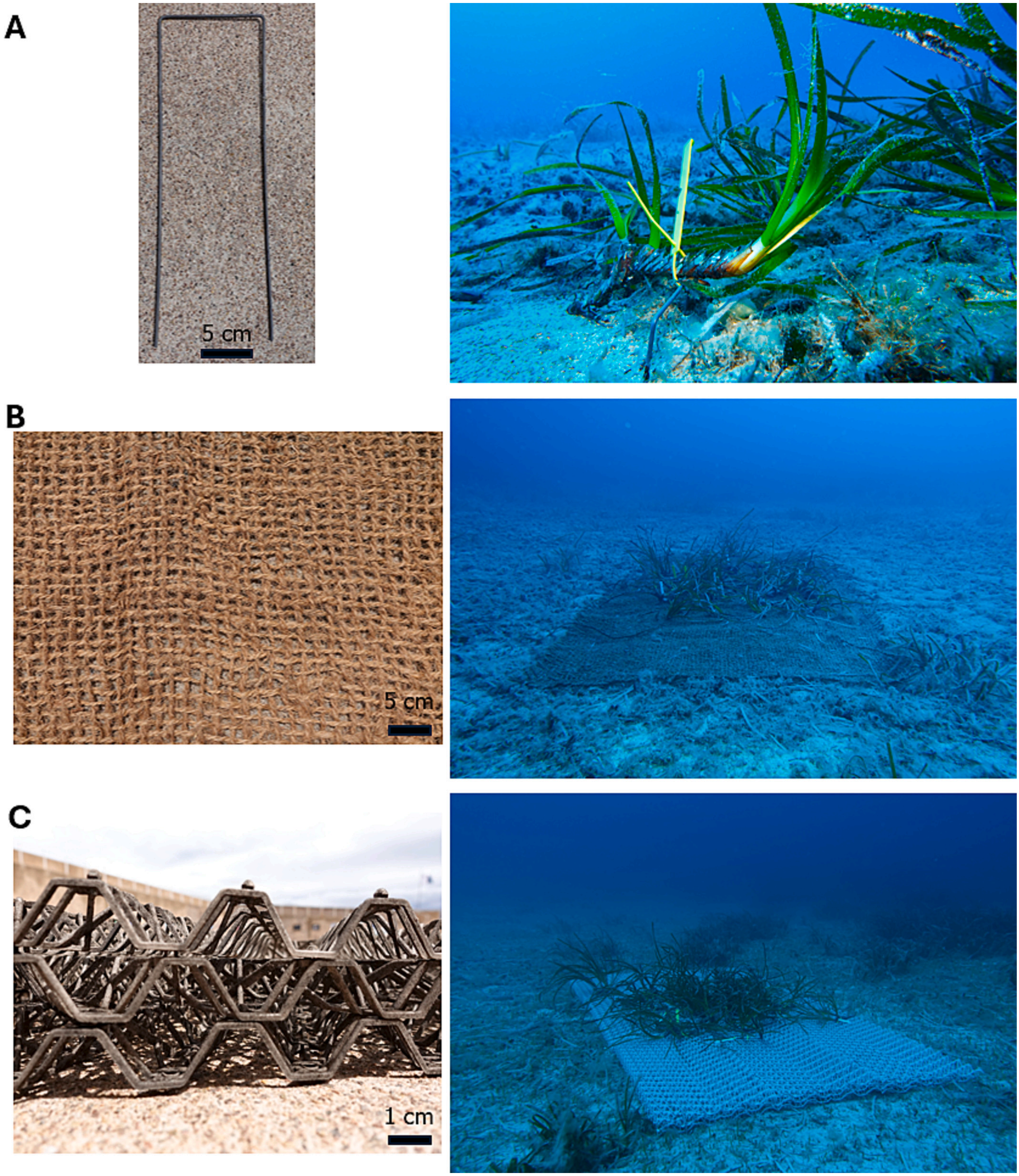

Fig. 2. The three transplantation methods used in this study: (A) Iron staple, (B) coconut fiber mat and (C) BESE element.

consisted of storm-fragments collected from natural accumulation areas located in natural sandy intermattes within *P. oceanica* meadows (Abadie et al., 2015; Gobert et al., 2016). These were collected during SCUBA dives at depths ranging from 6 to 28 m (Fig. 3A). A smaller portion (231 fragments) of the total cutting pool was manually excised from the erosion edges of natural sandy intermattes at 15 m depth near STARESO (Gobert et al., 2016) (Fig. 3B). These intermatte cuttings were specifically included to enable comparison of survival rates and morphological traits between the two donor sources. The harvesting of those cuttings from the erosion edges of natural sandy intermattes was primarily guided by sustainability considerations, aiming to minimize the disturbance to the core of healthy donor meadows. This approach

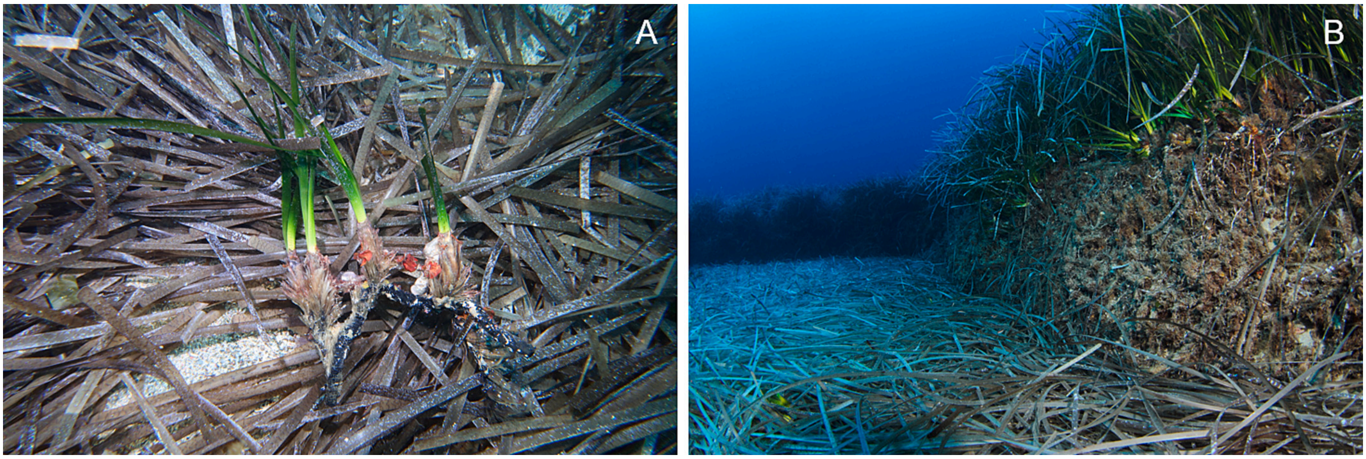

Fig. 3. The two donor sources used in this transplantation pilot study: (A) Storm-fragment laying on the seafloor, and (B) erosion edge of a natural sandy intermatte (©STARESO/Arnaud Abadie).

aligns with previously published observations indicating that erosion edges naturally contribute to the production of storm-fragments, as vertical matte notches erode and release pieces of rhizomes (Gobert et al., 2016). Moreover, *P. oceanica* shoots collected from erosion edges do not exhibit significantly lower photosynthetic activity, leaf surface area or leaf biomass compared to those from continuous meadows at 15 m depth (Abadie et al., 2017; Lapeyra et al., 2016). Furthermore, erosion edges tend to be dominated by plagiotropic rhizomes (up to 60 %; Lapeyra et al., 2016), which are particularly suitable for transplantation due to their horizontal growth form and more rapid growth rates compared to orthotropic rhizomes (Molenaar and Meinesz, 1995). All fragments (both storm-derived and intermatte cuttings) were harvested within Calvi Bay, in close proximity to the transplantation sites, to ensure the preservation of local genetic integrity.

The cuttings were maintained in outdoor flow-through seawater aquaria until their initial selection, which was based on rhizome length, number of shoots and visually assessed health condition (leaf necrosis and biting marks). Only cuttings bearing at least 3 shoots and a plagiotropic rhizome of at least 15 cm in length were retained, while those exhibiting excessive leaf necrosis were excluded. For each planting unit type (i.e. iron staples, cononut fiber mats and BESE elements) at each experimental site, 33 cuttings were attached using cable ties, comprising 22 storm-fragments and 11 intermatte cuttings. The cuttings were transplanted close together, with rhizomes spaced approximately 10 cm apart, a configuration shown to promote optimal survival and growth (Molenaar and Meinesz, 1995). The planting units were installed approximately 2 m apart from each other. In total, each experimental sites contained 99 transplants, resulting in an overall total of 693 *P. oceanica* transplants. All transplanted cuttings were labelled with small tags attached around the rhizomes by means of cables ties to allow for the monitoring of their survival over time.

2.3. Sampling strategy and morphological traits measurements

Before the start of the transplantation work, 20 cuttings, including both storm-fragments and cuttings from intermattes, were preserved for biometric measurements and further laboratory analyses. In addition, 20 *P. oceanica* fragments were collected from nearby reference meadows at depths of 20 m and 28 m. This sampling provided a T0 baseline, allowing comparisons between the cuttings and the control meadows prior to transplantation. Following transplantation, six monitoring campaigns were conducted at 3, 12, 15, 24, 27, and 36 months post-transplanting. These campaigns were carried out three times in spring (April–June; 12, 24 and 36 months post-transplanting) and three times in fall (September–October; 3, 15 and 27 months post-transplanting). During each monitoring campaign, the total number of foliar shoots per planting unit was recorded. Survival rate was assessed based on the presence of at least one living shoot per rhizome. Survival data were recorded in a binary format, with (1) indicating a living transplant and (0) indicating a dead one. At each experimental site ($n = 7$), 12 shoots were collected from transplants for biometric measurements, resulting in a total of 84 sampled shoots per campaign. Additionally, 10 control shoots were collected from surrounding meadows at 20 m and 28 m depths and brought back to the laboratory for further examination. All the shoots were sampled using the Non-Destructive Shoot sampling Method (NDSM) as recommended by Gobert et al. (2020). For each sampled shoot, the number of leaves was counted, and the length and width of each leaf were measured. Epiphytes were scraped from all leaves using a ceramic scalpel blade. The leaves were then oven-dried at 60 °C for 48 h and weighed to determine their dry biomass.

Furthermore, 36 months after transplantation, six cuttings per experimental site ($n = 42$) were harvested for rhizomes and root morphological traits measurements. The samples were carefully excavated using small hand tools to preserve the integrity of the root systems. The same procedure was applied to five *P. oceanica* fragments collected from the control meadow at 20 m depth and five from the control meadow at 28 m depth. In the laboratory, the collected plants were gently rinsed with seawater to remove fine sediment particles from the root systems. For each sampled individual, the number of primary and lateral roots was counted. The following morphological traits were measured: maximum width (i.e. maximum horizontal spread) and maximum rooting depth (i.e. maximum root length) of the root system, as well as the length of the plagiotropic rhizome (Fig. S2).

Roots were arranged on grid paper and photographed. The resulting images were analysed using the SmartRoot plugin in ImageJ software version 1.8.0_345 (Lobet et al., 2011). Image data were then used to calculate the total root length of each individual root system. Subsequently, the entire root system was oven-dried for 48 h at 60 °C and weighed to determine dry biomass. To account for variation in rhizome lengths among samples, all measurements were normalized to the length of the individual rhizome. Accordingly, the number of primary and lateral roots is expressed per centimetre of rhizome (cm^{-1}), biomass is reported as grams of dry weight per centimetre of rhizome ($gDW.cm^{-1}$), and total root length, maximum horizontal spread, and maximum rooting depth are expressed as dimensionless ratios.

2.4. Cost-efficiency analysis

To identify the most cost-effective transplantation method and assess its potential for upscaling, a cost-efficiency analysis was conducted.

Specifically, the planting cost per unit area (€.m^{-2}) was calculated based on the unit price and dimensions of the three materials tested. A planting density of 22 transplants per m^2 was considered, in accordance with the experimental design. This surface-based cost enables direct comparison between the different transplantation materials, assuming an equal number of cuttings transplanted over the same surface area. To account for the effectiveness of each transplantation method, the cost per planted surface area was adjusted by incorporating the survival rate associated with each technique. Assuming an initially planted area of 1 m^2, the remaining area 36 months post-transplantation reflects the survival rate and represents the effectively restored surface. Accordingly, the initial cost per planted m^2 was divided by the survival rate to obtain the cost per m^2 of *P. oceanica* meadow effectively restored after 36 months.

2.5. Data analysis

To assess the effects of the different experimental treatments on the survival of cuttings, the number of shoots per planting unit, and leaf morphological traits, Generalized Linear Mixed Models (GLMMs) were used. These models are well suited for handling discrete, non-negative data such as count data, and allow the inclusion of experimental site as random factor to account for variability among the seven sites (Fig. 1). A binomial distribution was used for the response variable survival rate. Fixed factors included in the GLMMs were 'Transplantation method' (three levels: iron staple, coconut fiber mat, and BESE element), 'Donor source' (two levels: intermatte cutting and storm-fragment), 'Bathymetry' (two levels: shallow and deep), and 'Months post-transplanting' (six levels: 3, 12, 15, 24, 27, and 36 months). For the response variable average number of shoots per planting unit, a negative binomial distribution was used and the fixed factors used were 'Transplantation levels', 'Bathymetry' and 'Months post transplanting'. A Poisson distribution was used for the number of leaves per shoot, and a Gamma distribution with a log link function was used for the leaf surface area, the maximum leaf length and the dry weight. The same set of fixed factors as in the survival rate model was included in the GLMMs for these leaf morphological traits. Because the experimental sites were nested within the bathymetric levels, a nested random structure (1|Bathymetry/Site) was specified in the GLMMs. GLMMs were built using the *glmer* function from the *lme4* package in RStudio software version 4.3.2 (RStudio Inc., Boston, MA, USA). Model selection was guided by Akaike's Information Criterion (AIC), progressively removing non-significant terms based on statistical criteria until no further variables could be eliminated. Overdispersion was assessed by comparing the residual deviance to the residual degrees of freedom. To test the statistical significance of differences between treatments, estimated marginal means (EMMs) were computed using the *emmeans* function in RStudio, applying Bonferroni correction to adjust *p*-values for multiple comparisons.

To compare the leaf morphological traits of the cuttings with the control plants, the normality and linearity of the residuals were assessed by visually inspecting the residuals versus fitted values plot and performing a Shapiro-Wilk test, while the homogeneity of variances was checked using Levene's test. Data assumption checking was conducted using RStudio software. Since the data were not normally distributed, PERMANOVAs were used to compare the transplants to the control meadows over time. PERMANOVAs were computed using the fixed factors 'Transplantation effect' (two levels: control meadow, transplant), 'Months post-transplanting' and their interaction. The root morphological traits were assessed only 36 months after transplanting and compared between transplants and control meadows. PERMANOVAs were also computed for the following root morphological traits: number of adventitious roots, maximum horizontal spread, maximum rooting depth, total root length, and total root biomass (dry weight). Since the factor 'Donor source' and the interaction with 'Transplantation method' and 'Bathymetry' were not significant for any of the root morphological traits, they were excluded from the PERMANOVA design to reduce the number of interactions and model complexity. Therefore, the final PERMANOVA design for the root morphological traits included the fixed factors 'Transplantation method and effect' (four levels: iron staple, coconut fiber mat, BESE element, and control meadows) and 'Bathymetry'. Prior to running the PERMANOVAs, a resemblance matrix based on Euclidean distances was calculated on untransformed data. The effects of the factors on each response variable were assessed using permutation tests applied to the residuals of a reduced model, with analyses based on Type III partial sums of squares. The number of permutations was set to 999 and Monte Carlo tests were performed when the number of permutations was fewer than 100. PERMANOVAs were performed using the PRIMER-E + PERMANOVA software version 7.0.24 (PRIMER-E, Auckland, New Zealand). All the differences were considered statistically significant when $p < 0.05$. All values were reported as mean ± standard error.

3. Results

3.1. Survival rates and shoot counts

The survival rate of *P. oceanica* cuttings transplanted in spring 2022 was monitored over a 36-month period and revealed contrasting responses depending on the experimental treatments. First, the donor source of the cuttings had no significant effect on survival (Fig. S3), nor did any of its interactions with the three other experimental factors. As a result, this factor was excluded from the final GLMM. Neither the transplantation method nor the bathymetry showed a significant main effect on survival rate. However, significant interaction effects were detected between transplantation method and time since transplanting ($p < 0.001$; F = 3.85), as well as between transplantation method and bathymetry ($p < 0.001$; F = 10.30) (Fig. 4A). Finally, time since transplanting had a strong and significant effect on survival rate ($p < 0.001$; F = 59.52). Thirty-six months after transplantation, survival rates revealed marked contrasts, with higher survival observed at deep sites compared to shallow ones (Fig. 4A). At shallow sites, cuttings fixed to BESE elements exhibited significantly higher survival rates than those fixed with iron staples and coconut fiber mats ($p = 0.020$ and $p < 0.001$, respectively). Survival was also significantly different between cuttings attached with iron staples and those with coconut fiber mats ($p < 0.001$) (Fig. 4A). At deep sites, survival rates were significantly higher for BESE elements compared to coconut fiber mats ($p < 0.001$), but no significant difference was found between BESE elements and iron staples (Fig. 4A). However, iron staples resulted in significantly higher survival than coconut fiber mats ($p < 0.001$) (Fig. 4A). Thirty-six months post-transplanting, the highest survival rate was recorded for iron staples at deep sites (82.58 ± 0.03 %), while the lowest was observed for coconut fiber mats at shallow sites (31.31 ± 0.05 %) (Fig. 4A).

The total number of shoots per planting unit was monitored across all experimental sites for the entire 36-months monitoring period. The number of months post transplanting had a significant effect on the total number of shoots per planting unit ($p < 0.001$; F = 33.1944), as did the interaction between transplantation method and months post transplanting ($p < 0.001$; F = 4.1121) (Fig. 4B). In contrast, bathymetry had no significant influence on the total number of shoots per planting unit. Regardless of the transplantation method used, a general decline in the total number of shoots per planting unit was observed over time (Fig. 4B). At 36 months post transplanting, shoot counts were significantly higher on BESE elements and iron staples compared to coconut fiber mats ($p < 0.001$ for both). However, there was no significant difference in shoot numbers between BESE elements and iron staples.

3.2. Leaf morphological traits

GLMMs were performed to assess the influence of transplantation method, donor source, bathymetry and months post transplanting on the leaf morphological traits of the *P. oceanica* transplants. For both the

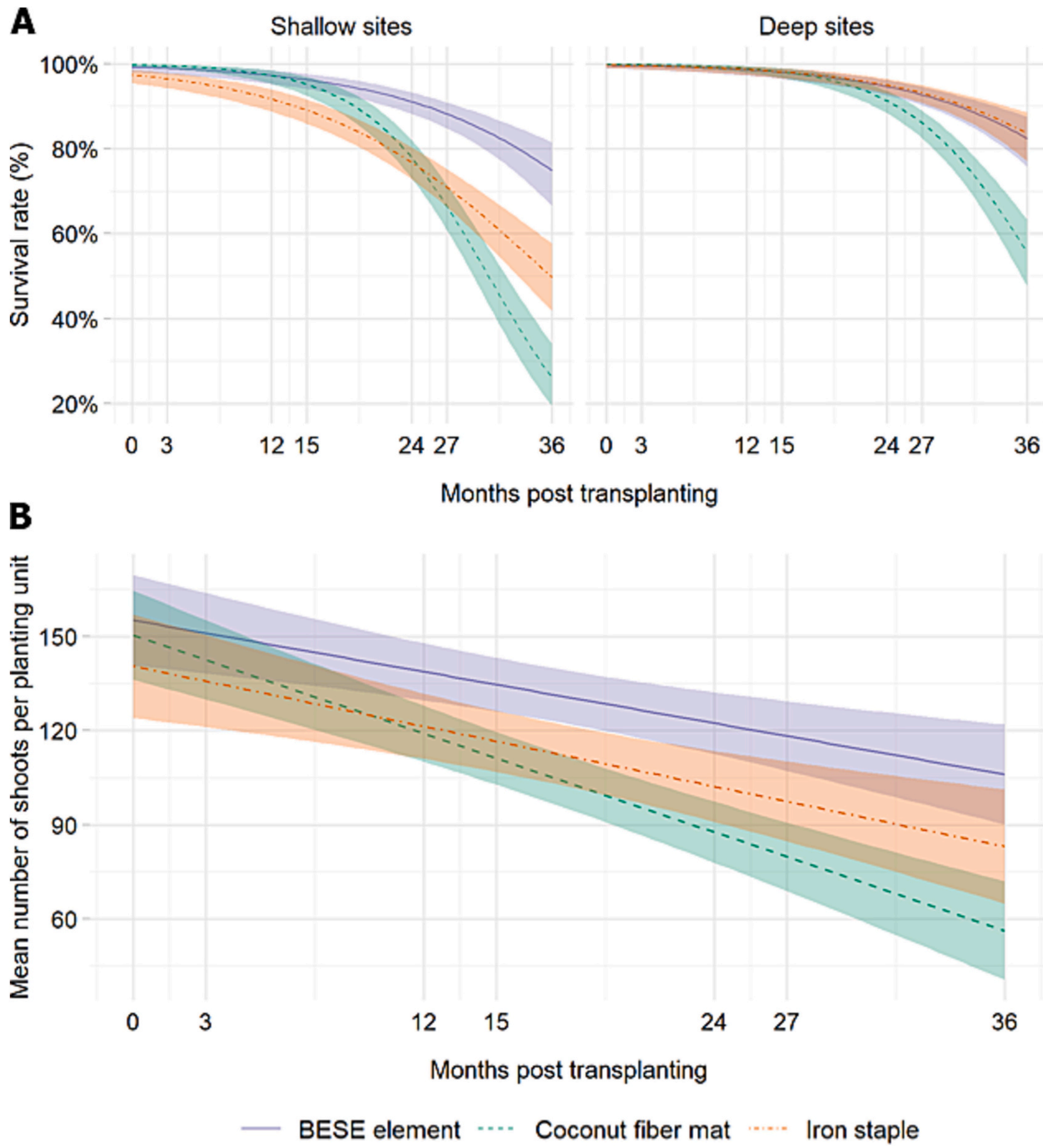

Fig. 4. Temporal dynamics of (A) transplanted cuttings' survival rates according to transplantation method at shallow and deep sites and (B) mean number of shoots per planting unit according to transplantation method. Shaded areas around the curves represent 95 % confidence intervals.

number of leaves per shoot and the dry weight, none of the four response variables had a significant effect. The maximum leaf length was only significantly influenced by the months post transplanting ($p < 0.001$; $F = 6.578$), with significant differences each time between spring and fall monitoring campaigns. The leaf surface area was significantly influenced by the bathymetry ($p = 0.014$; $F = 8.4173$) and the months post transplanting ($p < 0.001$; $F = 10.4409$), with significant differences each time between spring and fall monitoring campaigns. The PERMANOVAs performed with the factors transplantation effect and months post transplanting highlighted several significant differences between transplants and control meadows over the 36 months of monitoring. The number of leaves, maximum leaf length, leaf surface area and biomass were significantly influenced by the transplantation effect, the months post transplanting, and the interaction between the two factors (Fig. 5, Table S1). The transplants had a higher number of leaves at the time of transplanting compared to control meadows, followed by a similar number of leaves 3 months and 12 months post transplantation. After 15 months, the transplants had less leaves per shoot than the control meadows (Fig. 5, Table S2). The maximum leaf length was always higher for the control meadows compared to the transplants (Fig. 5, Table S2). The leaf surface area was similar for both transplants and control meadows at the time of transplanting, but three months after transplantation the leaf surface area of the transplants was significantly lower than the control meadows (Fig. 5, Table S2). Finally, the control meadows had a significantly higher biomass than transplants for all monitoring campaigns, except 12 months post transplanting when there was no significant difference (Fig. 5, Table S2).

3.3. Root morphological traits

The six root morphological traits investigated in this study were all significantly influenced by the transplantation method + effect (Table S3). Strong differences were found with control meadows having a much more developed root system than the transplants (Fig. 6, Table S4). Significant differences were also found between the transplants according to the transplantation method, with the transplants attached to the iron staples having a much more developed root system than transplants on the coconut fiber mats or the BESE elements (Fig. 6,

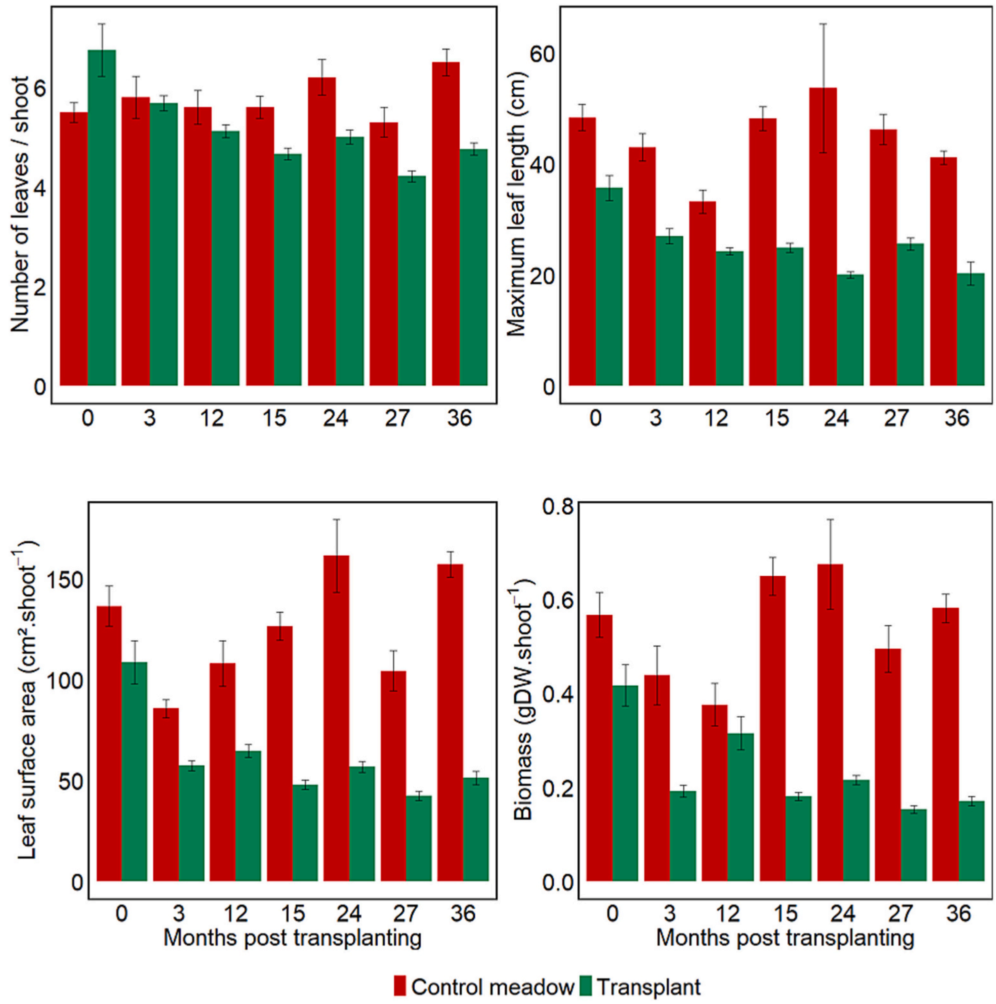

Fig. 5. Mean number of leaves, maximum leaf length, leaf surface area and biomass of *P. oceanica* transplants and control meadows. Vertical error bars represent standard errors.

Table S4). No significant differences in root morphological traits were found between the transplants on the coconut fiber mats and the BESE elements (Fig. 6, Table S4). The number of primary roots was also significantly influenced by the bathymetry, with higher values at the deep sites (Table S3). Moreover, the number of lateral roots was significantly influenced by the interaction between transplantation method + effect and bathymetry (Table S3). For the shallow sites, the control meadow plants had a more developed compared to the transplants with the iron staples, which had more lateral roots compared to the transplants on the coconut fiber mats and the BESE elements (Fig. 6, Table S4). For the deep sites, there was no significant difference in the number of lateral roots between control meadows and iron staples, but both still had significantly more lateral roots than coconut fiber mats and BESE elements (Fig. 6, Table S4). It is also noteworthy that no lateral roots were observed on transplants attached to BESE elements or coconut fiber mats at shallow sites. A similar pattern was observed at deep sites, except that a very small number of lateral roots were present on transplants anchored with coconut fiber mats (Fig. 6).

3.4. Cost-efficiency analysis

The unit costs of the three transplantation materials differed considerably, leading to substantial variations in the cost per m^2 transplanted. BESE elements were by far the most expensive, followed by coconut fiber mats, whereas iron staples represented the most economical option. Although survival rates vary among the three transplantation methods, the cost trends remain consistent when comparing both the costs per m^2 transplanted and the cost per m^2 effectively restored after 36 months. Iron staples resulted in the lowest cost per effectively restored m^2 at both shallow and deep sites (Table 1).

4. Discussion

In recent years, numerous efforts have been made to transplant *P. oceanica*, reflecting a growing interest in the conservation and restoration of marine ecosystems (Boudouresque et al., 2021; Pansini et al., 2022). However, several knowledge gaps remain and need to be addressed to improve the success of *P. oceanica* meadow restoration projects. Among these, the comparison of donor sources for planting material (donor meadow vs storm-fragment) and the development of sustainable methods for transplant fixation on the seafloor are two key research areas (Pergent-Martini et al., 2024) investigated in this study. This experimental work aimed to address these gaps by transplanting a total of 693 *P. oceanica* cuttings onto dead matte at a recipient site in the Bay of Alga (Calvi, Corsica). The three-year monitoring conducted during this initial study identified the most effective transplantation method and donor source, and confirmed the suitability of the site for the implementation of a large-scale restoration project (Boudouresque et al., 2021; Pergent-Martini et al., 2024).

P. oceanica transplantation projects have relied on rhizome fragments either directly harvested from donor meadows (e.g. Bacci et al., 2024; Calvo et al., 2021) or collected as storm-fragments of unknown

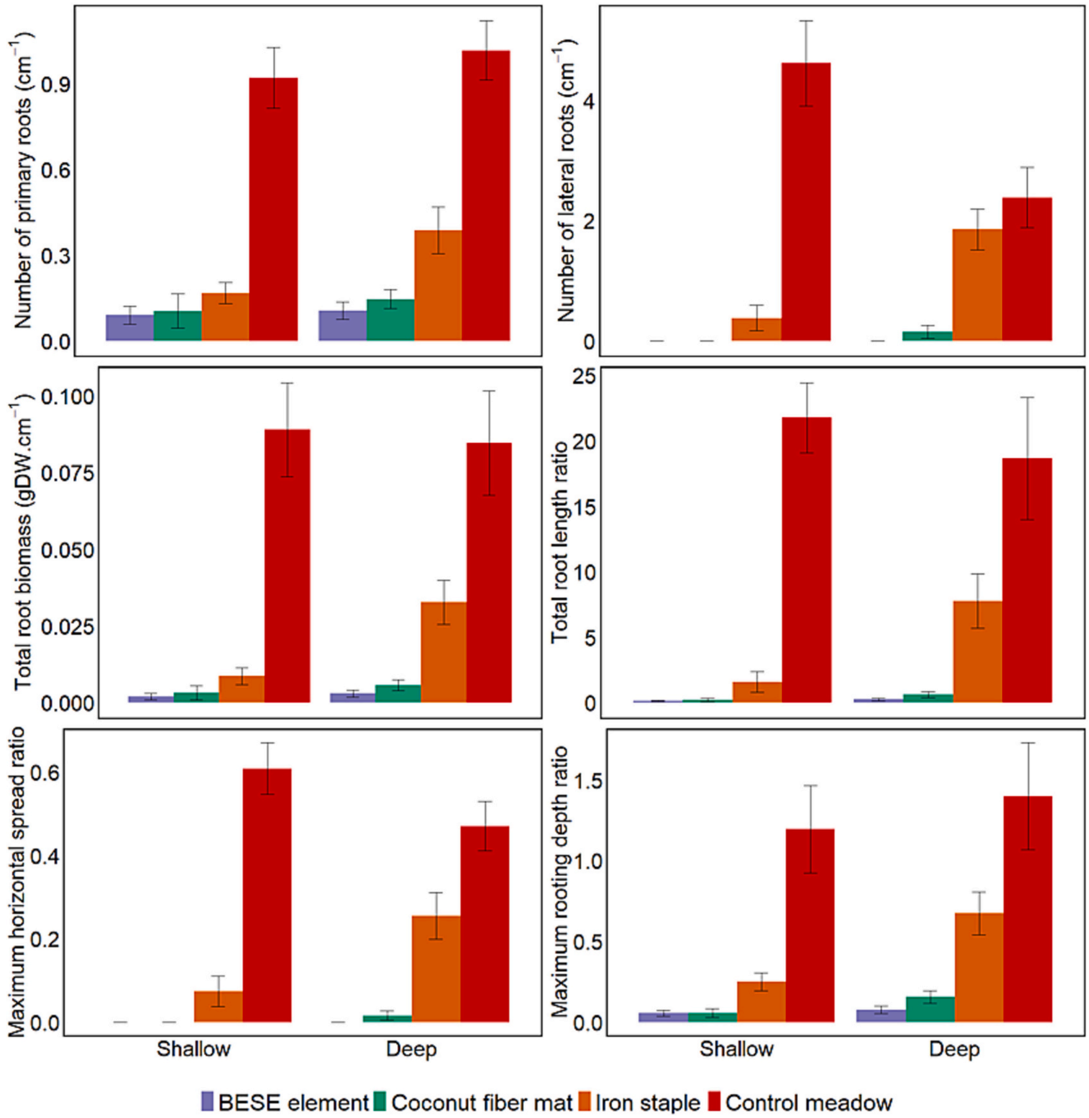

Fig. 6. Mean number of primary roots, number of lateral roots, total root biomass, total root length ratio, maximum horizontal spread ratio, maximum rooting depth ratio of *P. oceanica* transplants (according to the different transplantation methods) and control meadows as a function of bathymetry. Vertical error bars represent standard errors.

Table 1
Cost-efficiency comparison of transplantation methods.

Transplantation method	Unit cost (€)	Unit size (m^2)	Cost/ transplanted surface (€.m^{-2})	Mean survival		Cost/restored surface after 36 months (€.m^{-2})	
				Shallow	Deep	Shallow	Deep
BESE element	21.0	0.42	50.0	0.788	0.818	63.4	61.1
Coconut fiber mat	8.1	1	8.1	0.313	0.538	25.9	15.1
Iron staple	0.3	NA	6.6	0.566	0.826	11.7	8.0

origin (i.e. depth, substratum), typically found drifting on the seafloor and accumulating at the edges of meadows or in natural sandy intermattes (e.g. Castejón-Silvo and Terrados, 2021; Mancini et al., 2021; Piazzi et al., 2021;). To the authors' knowledge, this is the first *P. oceanica* transplantation project to experimentally compare the performance of these two donor sources as planting material under similar environmental conditions. Results from the 36 months of monitoring revealed no significant differences between storm-fragments and intermatte cuttings in terms of survival rate, leaf and root morphological traits. These findings indicate that, when transplanted under similar environmental conditions, the origin of planting material (donor meadow vs storm-fragment) does not significantly influence transplant performance within the studied timeframe. Storm-fragments, once detached from their original meadow, retain the capacity to re-establish and thrive when reintroduced (Almela et al., 2008; Balestri et al., 2011). As a non-destructive alternative to harvesting fragments from donor meadows, storm-fragments should be prioritized as planting material in restoration initiatives. The use of cuttings collected from donor meadows should only be considered when storm-fragments availability in the study area is insufficient to support the restoration of degraded sites. Furthermore, we recommend prioritizing collection from erosion edges of natural sandy intermattes rather than from other

P. oceanica seascape types (Abadie et al., 2015; Gobert et al., 2016). These intermattes undergo natural dynamics of erosion and recolonization, driven by orbital bottom currents eroding the meadow and creating vertical matte edges (Gobert et al., 2016). Harvesting *P. oceanica* cuttings at these erosion edges has a lower ecological impact, as the action of currents in these zones naturally leads to the formation of storm-fragments from exposed rhizomes (Fig. 3B). As a last resort, and only when the area targeted for restoration is large relative to the total surface area of existing *P. oceanica* meadows in the study area (Boudouresque et al., 2021), harvesting fragments from other parts of the donor meadow may be considered. In such cases, extraction should not exceed the threshold of one rhizome per m^2 of donor meadow as recommended by Pergent-Martini et al. (2024).

While the donor source had no significant influence on transplant survival 36 months after transplantation, the method used to anchor the cuttings plays a more decisive role, influencing both survival rates and root system development. This study compared the use of biodegradable structures (i.e., BESE elements and coconut fiber mats) as anchoring material with individual iron staples as transplantation methods. The structural complexity provided by BESE elements and coconut fiber mats mimics emergent traits (Piazzi et al., 2021; Temmink et al., 2020), such as dense aggregations of roots and rhizomes. These traits are known to promote self-facilitation processes naturally generated by established conspecifics, and were hypothesized to reduce physical stress and enhance long-term establishment of the transplants (Temmink et al., 2020). To define if the transplantation methods used were successful or not, transplantation success was defined as a survival rate $\geq$ 50 % (Danovaro et al., 2025) three years after transplantation (Molenaar and Meinesz, 1995). Survival outcomes differed between transplantation depths. At shallow sites, coconut fiber mats did not meet the success threshold, whereas both BESE elements and iron staples were successful, although iron staples had a survival rate (56.57 $\pm$ 0.05 %) only slightly above the defined threshold. At deeper sites, both BESE elements and iron staples were highly successful, with survival rates exceeding 80 %. Coconut fiber mat also achieved a survival rate above the threshold (53.79 $\pm$ 0.04 %), but with a lower survival rate than the other two methods. Similar survival rates for cuttings transplanted on coconut fiber mats were obtained by Piazzi et al. (2021) who tested the same methodology. However, contrary to the recommendations of Piazzi et al. (2021), our results show that coconut fiber mats were the least effective method at both tested transplanting depths. In addition to lower survival rates, coconut fiber mats also resulted in significantly lower shoot abundance compared to both BESE elements and iron staples. Finally, the cost-efficiency analysis does not support the use of coconut fiber mats, which should therefore be excluded from consideration in large-scale restoration projects under similar environmental conditions.

Although BESE elements and iron staples exhibited similar survival rates at deep sites 36 months after transplantation, iron staples showed lower survival rates at shallow sites, whereas BESE elements maintained similar survival rates across both depths. Previous evidence indicate that the survival rate of *P. oceanica cuttings* transplanted at different depths is quite variable. For instance, higher survival rates were reported at shallower depths (8–12 m) compared to deeper sites (17–21 m) in Mancini et al. (2021), suggesting that increased light irradiance may promote higher survival at shallower depths. However, a large-scale transplantation project using iron staples on dead matte reported 79 % survival two years after transplantation, with no significant differences between shallow (8–10 m) and deep sites (18–23 m) (Mancini et al., 2022). Similarly, Castejón-Silvo and Terrados (2021) observed no differences in survival rates between cuttings transplanted at 15, 20 and 25 m depth. Our results suggest that differences in light intensity between shallow and deep sites did not significantly influence cutting survival 36 months after transplantation, highlighting *P. oceanica* ability to acclimate to a range of light conditions as observed in previous studies (Boulenger et al., 2024; Dattolo et al., 2017;). It is also noteworthy that most of our cuttings were transplanted at deeper depths than their origin. Specifically, intermatte cuttings were collected at 15 m, while storm-derived fragments originated from a depth range of 6 m to 28 m. Previous studies have shown that transplanting *P. oceanica* cuttings to deeper waters than their origin may result in reduced survival (Genot et al., 1994; Molenaar and Meinesz, 1995). However, more recent research reports contrasting outcomes, with high survival rates even at increased depths (Boulenger et al., 2024; Mancini et al., 2022), and with evidence of photosynthetic acclimation to ambient light conditions (Boulenger et al., 2024). Interestingly, studies reporting lower survival rates relied on orthotropic rhizomes (Genot et al., 1994; Molenaar and Meinesz, 1995), whereas those showing little or no depth-related impact used plagiotropic shoots (Boulenger et al., 2024; Mancini et al., 2022). These findings suggest that while transplanting cuttings at similar depths may facilitate acclimation due to pre-existing physiological adaptations, it is not a strict requirement, particularly when using plagiotropic rhizomes and when donor and recipient sites are located within the same bay and experience comparable environmental conditions. It is therefore likely that the lower survival of cuttings anchored with iron staples at shallow sites is due to increased hydrodynamic stress. Shallower areas typically experience higher hydrodynamic energy, which decreases with depth (Bonamano et al., 2021). This was further supported by monitoring *P. oceanica* natural recolonization, which showed more pronounced erosion at shallow sites compared to deeper ones (Boulenger et al., 2025a). Iron staples possess lower structural rigidity compared to BESE elements, potentially explaining their reduced performance under high-energy conditions, while their similar performance at deeper sites could be attributed to the reduced hydrodynamic forces (Table 2). Moreover, the cuttings were initially secured to the horizontal section of the iron staples using plastic cable ties wrapped around the rhizome. However, this method proved detrimental, as wave action and currents could cause the ties to cut into the rhizome, leading to transplant damage and loss. After observing these negative effects, we replaced this approach by simply positioning the

Table 2
Summary of the main limitations and site-specific advantages of iron staplesand BESE elements as transplantation methods for *P. oceanica* restoration.

Transplantation method	Limitations	Site-specific advantages
Iron staple	– Lower performance under high hydrodynamic conditions – Requires manual insertion in dead matte; limited applicability on unconsolidated substrates	– High survival rates on intact matte substrates under low hydrodynamics. – Promotes robust root development, enhancing anchorage and belowground biomass accumulation – High cost-efficiency (10× cheaper than BESE) – Minimal introduction of exogenous material into the environment – Can be removed after a couple of years when root system is sufficiently developed
BESE element	– Delayed root development (limited root traits after 36 months) – High material costs – Physically elevate cuttings (~6 cm above dead matte), possibly reducing plant–microbe interactions and root system development	– Consistent survival across depth gradients (20–28 m), including high-hydrodynamic zones ➔ Biodegradable structure mimics natural root-rhizome matrix and may facilitate conspecific aggregation/self-facilitation in high-stress areas (e.g., Temmink et al., 2020) – Suitable for degraded matte or unstable sandy/gravel substrates where staples are not applicable

iron staple directly over the rhizome without using cable ties. This adjustment minimized shear stress and resulted in improved anchorage stability over time. These results emphasize the importance of testing different transplantation methods under varying environmental conditions, and the need of site-specific restoration designs as no universally optimal solution exists.

Another key difference between transplantation methods lies in the development of root morphological traits. Establishing a functional root system is crucial for transplants to provide nutrient supply to meet physiological needs (Lepoint et al., 2004), withstand hydrodynamic stress and ensure long-term survival (Lepoint et al., 2004; Vangeluwe et al., 2004). For all six root traits measured three years after transplantation, significantly greater development was observed in cuttings anchored with iron staples (Table 2). Initially, the cuttings initially lacked a developed root system, and three years' post-transplantation, little to no root development was observed in cuttings fixed with BESE elements or coconut fiber mats. Previous studies have shown that root formation in *P. oceanica* rhizome fragments primarily occurs during spring and summer and typically takes from 3 to 12 months (Balestri et al., 2011). However, Castejón-Silvo and Terrados (2021) reported that the development of a fully functional root system in transplanted cuttings may take up to two years. Our findings indicate that under certain conditions, it can take more than three years to grow an effective root system, as observed in transplants anchored with BESE elements and coconut fiber mats (Table 2). This delay could be attributed to a limited availability of internal reserves in the transplants on the coconut fiber mats and BESE elements, which may impede root formation (Lepoint et al., 2004; Vangeluwe et al., 2004). Nonetheless, this limitation is thought to primarily affect orthotropic rhizomes and may not apply to plagiotropic rhizomes as used in our study (Castejón-Silvo and Terrados, 2021). Moreover, there was no differences in the number of leaves, maximum leaf length, leaf surface area and leaf biomass between transplantation methods. Sandy substrates appear to promote the development of *P. oceanica* root systems (Balestri et al., 2015). Cuttings anchored with iron staples had direct contact between their rhizomes and the sediment, including the underlying dead matte (Fig. 2). In contrast, cuttings placed on coconut fiber mats are physically separated from the seafloor by the 5 mm thickness of the mat (Fig. 2). Similarly, BESE elements create a 6 cm elevation, resulting in a substantial gap between the transplants' roots and the dead matte (Fig. 2). These differences in spatial positioning likely modulate the degree of interaction between the roots and the surrounding sediment microbial pool, which is known to influence the recruitment and establishment of root-associated bacterial communities. Plants selectively recruit their microbiome from the surrounding soil or sediment, and the composition of this initial microbial pool plays a critical role in shaping root microbial assembly and plant performance (Cúcio et al., 2016;). Cuttings in closer proximity to the sediment may benefit from greater exposure to beneficial sediment-associated bacteria, whereas elevated cuttings are subjected to altered oxygen and nutrient gradients that could favour distinct microbial assemblages (Boulenger et al., 2025b). Moreover, plant exudates released by the roots in the surrounding sediment promote microbial colonization through chemotaxis, attracting beneficial microbial partners that enhance plant fitness within the seagrass rhizosphere (Crump et al., 2018; Sogin et al., 2022). However, such interactions may be diminished in cuttings placed on coconut fiber mats and BESE-elements due to their reduced initial contact with the sediment, potentially limiting early microbiome recruitment and establishment (Boulenger et al., 2025b). Given the potentially beneficial role of microbial interactions in seagrass ecology, further research is needed to better understand their influence on transplantation success and to assess how different transplantation methods may shape associated bacterial communities during the early stages of transplants' establishment (Corinaldesi et al., 2023). Metagenomic approaches offer valuable tools to investigate these dynamics at both phylogenetic and functional levels. Expanding in situ studies across habitats and environmental conditions will be crucial to fully integrate microbiome knowledge into effective restoration practices (Corinaldesi et al., 2023).

Based on these results, the use of iron staples is recommended as a transplantation method for *P. oceanica* restoration projects conducted on dead matte. Although BESE elements achieved survival rates high enough to be considered successful, the near absence of root development in transplants raises concerns about their long-term persistence. Moreover, the cost-efficiency analysis revealed that the use of BESE elements was the least cost-effective among the three tested methods, primarily due to their high material costs (Table 2). In comparison, iron staples were found to be nearly ten times more cost-effective. Nevertheless, BESE elements may represent a suitable solution under specific environmental conditions. Castejón-Silvo and Terrados (2021) demonstrated that iron staples do not support the successful recovery of *P. oceanica* meadows when transplantation is carried out on sandy or gravel substrates lacking underlying dead matte (Table 2), such as areas disturbed by underwater infrastructure works (e.g., power line installation). In cases where such interventions are unavoidable and affect matte areas, the addition of calcareous stones has been proposed as to promote natural recolonisation (Badalamenti et al., 2011) and to serve as a substrate for transplantation (Alagna et al., 2019). An alternative method, tested by Bacci et al. (2024), involved the use of cement blocks combined with metallic grid frames to transplant *P. oceanica* cuttings onto sandy sediments following pipeline installation. However, both methods present notable disadvantages, including high economic costs, greater handling difficulty due to the weight of the structures, and the introduction of substantial amounts of exogenous material (i.e., stones, cement) into the marine environment. In contrast, BESE elements may offer a suitable transplantation method for restoring *P. oceanica* meadows in areas where the matte has been degraded (Table 2). This approach has the advantage of using a fully biodegradable artificial substrate and allows for easier handling due to the lightweight nature of the material. Further research is needed to test the use of BESE elements in degraded matte areas and to determine whether the survival rates observed in our study are consistent under those environmental conditions.

The results of this study indicate that both iron staples and BESE elements achieved transplantation success after three year, as defined by survival thresholds. However, the same conclusion cannot be drawn regarding restoration success, which refers to the re-establishment of the structural and functional characteristics of the transplanted meadow in alignment with those of a natural reference site. Three main categories can be used to comprehensively assess restoration success: (1) seagrass structural attributes, such as canopy height, shoot density, and biomass; (2) ecological functions, including fish and invertebrate diversity and abundance, epiphytic colonization, and nursery habitat provisioning; and (3) biogeochemical functions, encompassing parameters such as water temperature, porewater nutrient concentrations, sediment granulometry, organic matter content, and sedimentation rate (Beheshti et al., 2021; Boulenger et al., 2025a; Castro-Fernández et al., 2025; Pergent-Martini et al., 2024). Among these, seagrass structural complexity is a particularly important driver, as it directly supports the recovery of both ecological and biogeochemical functions (Beheshti et al., 2021; Castro-Fernández et al., 2025). Thirty-six months after transplantation, significant differences in both leaf and root morphological traits were observed between transplants and control meadows. Leaf morphological traits remained relatively stable throughout the monitoring period, showing neither clear progression or regression when compared to the control meadow. The reduced leaf traits may reflect suboptimal environmental conditions, a possible relocation of internal resources from leaf production to rhizome horizontal growth (Lepoint et al., 2004), or increased leaf breakage due to greater exposure to water movement within a sparsely vegetated canopy, as typically occurs in transplanted areas lacking the structural buffering of dense natural meadows (Collier et al., 2009). These findings are consistent with those of Pansini et al. (2024), who reported that transplants across five different sites exhibited a consistently lower number of leaves and reduced leaf growth rates compared to reference meadows, persisting up to 36 months post-transplantation. Notably, even six years after transplantation, the maximum leaf length was still lower than control meadows. Similarly, a long-term study conducted 10 years after transplantation on disturbed sandy sediment showed that transplanted shoots had shorter and narrower leaves compared to natural meadows (Bacci et al., 2024). However, these results contrast with the findings of Calvo et al. (2021) and Mancini et al. (2021), who reported higher primary production (i.e., leaf growth rate, leaf length, shoot density) in transplanted meadows compared to control meadows within the first 48 months following transplantation. As suggested by Pansini et al. (2024), this may be due to the use of *P. oceanica* cuttings with an intact root system, which was lacking in our cuttings at the time of transplantation. This likely constrained early shoot development in our study, consistent with previous findings (Lepoint et al., 2004; Vangeluwe et al., 2004). This hypothesis is further supported by the root traits data, which revealed that transplants exhibited significantly smaller root systems compared to control meadows. The only exception was the number of lateral roots, which was comparable between transplants anchored with iron staples and control plants at deep sites. Longer-term monitoring is required to determine whether the leaf and root morphological traits of transplants will eventually converge with those of control meadows over time.

The various transplantation methods tested to date highlight persistent challenges in achieving full restoration success. This includes both the failure to reach the structural characteristics of natural meadows over the long term and the incomplete recovery of associated ecological functions and ecosystem services. In particular, the reduced leaf traits observed in transplants result in lower habitat complexity, thereby diminishing their nursery and habitat functions for numerous fish species (Castro-Fernández et al., 2025). To date, the simultaneous recovery of all three components of *P. oceanica* restoration success, namely structural attributes, ecological functions, and biogeochemical functions, has never been demonstrated in any transplantation study (Pergent-Martini et al., 2024). This highlights the urgent need for further research that integrates all of these dimensions into long-term monitoring programs (>10 years), in order to determine the time frame required for the full recovery of *P. oceanica* ecosystem functions following transplantation. Furthermore, it may be valuable to develop new assessment tools or adapt existing ones, such as the Ecosystem-Based Quality Index (EBQI; Personnic et al., 2014), to enable standardized and replicable evaluation of both structural and functional recovery in transplanted *P. oceanica* meadows.

Moreover, to promote the recovery of ecosystem functions, it is recommended to transplant with high shoot densities to enhance structural complexity. Furthermore, implementing large-scale planting is also advised, as it has been shown to improve restoration outcomes (van Katwijk et al., 2016) by enabling new transplants to overcome negative feedbacks in the system (e.g. hydrodynamic stress, sediment resuspension) (Maxwell et al., 2017). However, large-scale transplantation should only be considered after a thorough assessment of the local environmental conditions (e.g., hydrodynamics, substrate type, light availability, sedimentation, etc) and the natural recolonization dynamics at the restoration site (Boudouresque et al., 2021; Boulenger et al., 2025a). It is essential to first conduct a pilot trial using a limited number of cuttings to identify the most suitable restoration method(s) under the site-specific conditions. Only after validating the effectiveness of the selected approach(es) should large-scale transplantation be implemented. Finally, it is important to emphasize that the slow growth rate of *P. oceanica* makes direct comparisons with the restoration of other seagrass species challenging. A better management of anthropogenic pressures and the prioritization of the conservation of existing *P. oceanica* meadows must remain the central objectives. In addition, large-scale (>1 ha) restoration of *P. oceanica* is particularly difficult due to the high costs and workload involved, as well as the limited availability of donor material. For effective restoration, efforts should instead focus on reducing the fragmentation of degraded meadows, thereby boosting natural recolonization processes.

5. Conclusion

This study provides new insights into *P. oceanica* restoration by comparing the performance of different transplantation methods and donor sources at shallow and deep sites. The results demonstrate that storm-fragments are as effective as donor meadow cuttings in terms of transplant survival and morphological development, supporting their use as a sustainable, non-destructive alternative for *P. oceanica* restoration projects. Among the tested transplantation methods, iron staples emerged as the most cost-effective and biologically effective solution. BESE-elements, while yielding comparable survival rates, presented limitations in root development and economic feasibility. Coconut fiber mats, despite their biodegradability, performed poorly across most performance indicators and are not recommended for larger scale operations under similar environmental conditions. This study emphasizes the importance of conducting pilot experiments before any large-scale planting, in order to select the most appropriate method based on the environmental conditions of the degraded site. Moreover, the study reveals that transplantation success does not necessarily equate to ecological restoration success. Significant differences in both root and leaf morphological traits between transplants and reference meadows persisted after three years, potentially affecting habitat complexity and ecosystem function recovery. These findings highlight the importance of monitoring beyond survival metrics, focusing on long-term structural and functional convergence with natural meadows. Finally, given the species' inherently slow growth and limited donor material availability, restoration should remain a complementary tool to conservation, and not a substitute. The protection and long-term management of existing *P. oceanica* meadows must remain the priority.

CRediT authorship contribution statement

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

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.scitotenv.2025.180488.

Data availability

Data will be made available on request.

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