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Seagrass sod transplantation: A relevant tool for preventing the destruction of meadows in coastal construction projects

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A R T I C L E I N F O

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A B S T R A C T

We present a successful case of seagrass meadow transplantation on the scale of an industrial project, challenging the long-held belief that these ecosystems are "non-transplantable." Using a sod-based transplantation technique, we relocated 384 m^2 of *Posidonia oceanica* meadow from a construction site in 24 days in 2017 to mitigate the environmental impact of reclaiming six hectares of marine land for a new development in Monaco. The eight-year monitoring program (2017–2024) evaluated both structural and physiological parameters of the transplanted seagrass, along with the sediment chemistry in its surrounding environment. Despite nearby maritime construction works during two years, the transplanted meadow showed remarkable resilience, with its health indicators quickly aligning with those of the surrounding natural meadows. Three years after transplantation, the seagrass was flowering in synchrony with the natural meadow and after eight years, its area had expanded beyond the initial transplant, growing by 25,8 % in 2024. This outcome supports salvaging and subsequent transplantation as a viable, ecologically sound alternative to destruction and subsequent compensation measures in coastal development projects. By confirming the effectiveness of careful transplantation techniques, the study underscores that transplantation should be fully considered as a relevant mitigation measure in the Avoid-Mitigate-Compensate sequence.

1. Introduction

In shallow waters, seagrasses are flowering plants that form extensive meadows worldwide storing carbon, improving water quality, providing food and habitat, and acting as biological indicators (Short et al., 2007, 2016). These coastal habitats are complex, productive and harbor a high biodiversity (Unsworth et al., 2022). They provide highly valuable ecosystem services that contribute to human well-being and the security of coastal communities (Potouroglou et al., 2020). Preservation of seagrass meadows is especially challenging close to coastal cities that have been developing on the shore for a long time, taking the form of port towns and touristic hot spots serving intense commercial transactions through the well-established ancient sea routes (Koutsi and Stratigea, 2019). Due to numerous anthropogenic activities impacting seagrass meadows, such as coastal urbanization, eutrophication or anchoring, seagrass restoration is considered as a critical positive strategy to address the worldwide issue of seagrass decline (Montefalcone, 2024; Tan et al., 2020; Unsworth et al., 2024; Van Katwijk et al., 2016). Challenging choices might be required to determine the most effective planting approach, as various methods have shown both successful and unsuccessful results, often influenced by local environmental conditions (Unsworth et al., 2024; Van Katwijk et al., 2009). Seagrass restoration techniques can be classified according to the transplant units used for planting, namely adult plants, seedlings or seeds (Tan et al., 2020). Both seeds and seedlings can be transplanted in the same way, with (Mancini et al., 2024; Unsworth et al., 2019) or without (Ambo-Rappe, 2022; Maulidiyah et al., 2024) an anchoring system aiming to reduce their loss by hydrodynamic forces. Adult plants

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can be planted with or without the associated sediment. The sprig method, also referred to as cuttings transplantation in the literature, involves planting a rhizome with roots and aboveground shoots without sediment, and it can be planted with or without an anchoring system (Matheson et al., 2017; Rehlmeyer et al., 2024) . Many anchoring or stabilizing techniques have been used, ranging from heavy materials like concrete frames (Carannante, 2011; Cooper, 1982), to metallic, plastic, or biodegradable mesh or wires (Kidder et al., 2015; Rautenbach et al., 2024; Temmink et al., 2020), and cost-effective stakes and staples (MacDonnell et al., 2022; Mancini et al., 2021). The last method involves the transplantation of adult plants with associated sediment, with "plug" and "core" transplantation typically referring to small transplanted units (Matheson et al., 2023; McDonald et al., 2020), while the "sod" transplantation technique refers to much larger transplanted units and are often mechanically transplanted (Paling et al., 2001; Uhrin et al., 2009).

In the Mediterranean sea - often considered as a model ocean where ecological and human influences meet and strongly interact, posing a large and growing potential impact to marine biodiversity (Coll et al., 2010) - the endemic species of seagrass *Posidonia oceanica* plays a central role in the functioning of marine coastal environments, protects coasts from erosion and storms, and can sequester carbon thanks to the accumulation of its rhizomes and roots, called matte (Mateo et al. 2006; Monnier et al. 2021; Pergent-Martini et al. 2021). *Posidonia oceanica* meadows are protected at different levels (international, European, national, and local) in many countries around the Mediterranean (medposidonianetwork, 2024). However, their global decline over the last decades is well-documented (Boudouresque et al., 2009; De los Santos et al., 2019) even though some natural recoveries are reported following management actions (Bockel et al., 2024). Despite the significant ecological and economic value of *P. oceanica*, estimated at between €284 and €514 per hectare per year (Campagne et al., 2015) and reaching up to €21,660 per hectare per year (Scanu et al., 2022), its conservation is severely challenged by competing social and economic pressures to develop maritime infrastructures such as ports, housing and industry - projects that are often considered to be essential (Clark, 1997) and contribute to coastal modifications that can have an impact on the distribution of shallow *P. oceanica* meadows (Ferrari et al., 2025).

The case of the Principality of Monaco is emblematic. This city-state of 2 km^2 is the second smallest independent state in the world after the Vatican. Its population of 38,367 in 2023 (IMSEE-Monaco statistics) makes it the most densely populated sovereign state and it is pursuing its growth, generating essential needs in terms of housing and infrastructures (d'Hauteserre, 2001). As Monaco can only grow by expanding into its territorial waters, several offshore building operations have been conducted from early 20th century (Monaco Now, 2022). In 2014, Prince Albert 2 of Monaco announced the reclamation of 6 hectares from the sea, i.e., 3 % of Monaco's surface area, to build a new district called "Mareterra". Considerable resources and attention have been devoted to the project's environmental ambitions, making the Principality a laboratory for ecological engineering and leading the authorities to authorize an innovative intervention to try to save 384 m^2 of *P. oceanica* in the project area by sod transplantation. This operation was carried out as part of a voluntary complementary research project and was not included in the 'avoid, mitigate, compensate' (AMC) sequence of the project, as it was considered that no recognised transplantation method existed at the time. In this article, we describe the novelty of the transplantation method used, as well as the temporal dynamics of structural and physiological parameters of the transplanted meadows over eight years. We discuss the ethical value of developing such techniques to avoid the destruction of large seagrass beds. Finally, we argue that seagrass meadows transplantation should be fully recognized as a relevant mitigation measure within the AMC sequence worldwide, serving as the preferred solution to prevent destruction and pseudo-compensation such as through artificial reefs or nurseries.

2. Materials and methods

2.1. Study site and context

Considered to be one of the largest coastal construction projects in Europe this decade, the development of "Mareterra" required extensive marine work to build a 6-hectare platform on the sea between the Larvotto Marine Protected Area (MPA) to the east and the Spelugues MPA to the west (Fig. 1), from June 2017 to December 2019. The platform extends to a depth of 32 m seaward of the coastline, which was already filled between 0 and 17 m in the 1970s when the Larvotto district was developed (Fig. 2). The project affected 1 300 m^2 of seagrasses on the 110 000 m^2 present in the principality (1,18 %). The main phases of the work were as follows: (1) dredging 600 000 m^3 of sediment unsuitable for construction (06/2017 to 01/2018), (2) depositing 1.5 million tons of aggregate to create a base of 500 m (01/2018 to 06/2018), (3) placing 27 parallelepiped caissons of 18 m^2 on the base to form a belt (07/2018 to 07/2019), (4) filling the inside of the belt with 75.000 tons of sand to enable the construction of the superstructures (12/2018 to 12/2019).

2.2. Choice of the replanting zone

The replanting zone was situated in the Larvotto Marine Reserve (43.744393 N, 7.433857E), a marine protected area located 200 m from the donor zone (Fig. 1). This is an area of fine sand at a depth between 17.0 and 19.8 m, in the vicinity of a growing natural seagrass bed, at its lower depth limit. This site, previously occupied by a more extensive meadow, was severely degraded by the massive discharge of channeled rainwater directly from the coast between the 1930s and 1980s (Fig. 2). However, the construction of Monaco's sewage treatment system in the early 1980s, along with the redirection of rainwater away from the shore through a 295-meter-long outfall, created favorable conditions for natural, albeit slow, recovery. Owing to the slow and incomplete progress of natural regeneration of the seagrass meadow, intervention through ecological restoration was considered justified to accelerate the process of recolonisation by the seagrass meadows at this site. Therefore, in this area, transplantation was a typical ecological restoration operation that aimed to accelerate the natural recolonisation by *P. oceanica*.

2.3. Transplantation material

Posidonia sods were collected using an Optimal 880 tree spade transplanter modified for underwater work (i.e. electronic equipment has been removed). This transplanter allows plants to be harvested with their intact roots, and preserve the surrounding soil and associated microbiome, which supports several processes essential for robust plant growth and health (Saleem et al., 2019). The transplanter was operated by a DOOSAN DX300 LC excavator, fitted with two extensions that extend the arm to a length of 27 m. Four GoPro cameras (one frontal, two lateral, and one axial) were installed on the transplanter for monitoring from the operator's cab.

The excavator was loaded onto a self-elevating platform, which provided stability even in rough seas (Fig. 3). A second barge, equipped with a pump for digging holes, was used for replanting the seagrass sods. To keep the plants always submerged and avoid dessication, a mobile platform was designed that allowed baskets to be prepared out of the water and then submerged to deposit the samples (Descamp et al., 2017). A total of 480 baskets (i.e. 384 m^2 of *P. oceanica* meadow) were transplanted into the Larvotto Marine Reserve at a mean depth of 17.5 m.

Once the *Posidonia* sods were removed, they were placed in a specially made 'basket' of 100 cm in diameter (0.8 m^2) and 50 cm high (Fig. 4) to transport the sods to the replanting site. The baskets were made from a 10 mm round metal bar frame covered in coconut coir fabric, avoiding the loss of sediment during transportation while being porous and quickly biodegradable. Iron is not known to be a pollutant at

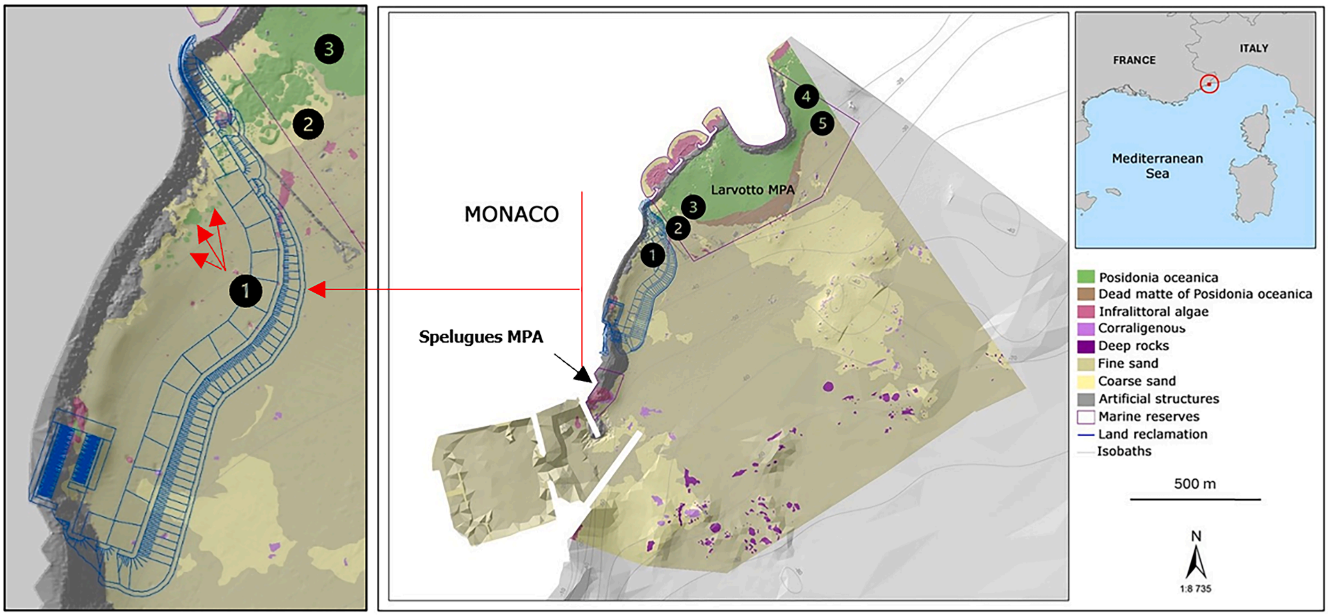

Fig. 1. Localisation of *Posidonia oceanica* donor meadow (1). Larvotto transplantation zone (2). Nearby meadow of reference (3). Distant meadow of reference (4). Distant meadow of reference at the lower limit (5). In blue the area of the construction project.

low concentration. It is a trace element necessary for photosynthesis, highly insoluble in seawater (Gledhill, 2012) and a nutrient limiting primary production in marine systems (Barbeau, 2006). However, for aesthetic reasons, the visible parts of the metal baskets were cut out using hydraulic pliers and removed from the sea in 2020.

2.4. Transport and replanting

For the transport, baskets were suspended at a depth of 10 m below 400 L buoys and then towed by boat to the replanting area. Basket-sized holes were created using a Toyo pump by commercial divers throughout the workshop. The baskets containing the sods were then placed in these holes. The transplants were installed along the south-west edge of the natural seagrass meadow, at its lower depth limit (Fig. 5).

2.5. Post-transplant care

Particular attention was paid to the plants after transplantation: the detached or loose rhizomes were secured to the substrate with 20 cm U-shaped metal clips. The leaves of the transplants and the nearby natural seagrass were cleaned three times between 2018 and 2019 to remove sediment deposits as a consequence of the ongoing construction works, and thus avoid deleterious effects on the photosynthesis of the seagrass. A stream of slightly pressurized water was gently sprayed on the leaves to remove accumulated sediments. For the transplants, the spray was applied manually using a fire hose by divers. For the surrounding natural *Posidonia* meadows, a cleaning machine was built consisting of a 6 m frame that supported a 200 mm metal tube equipped with eight fire-fighting nozzles angled 30 ° and 45° downwards powered by a 150 m^3/h motor-driven pump (Fig. 6). Baskets that were not level with the ground or were tilted were adjusted to make them perfectly level.

2.6. Long-term monitoring

The seagrass bed was monitored at three stations: The transplanted zone is referred to as 'Transplants', the nearby natural *Posidonia* meadow located 50 m from the transplanted zone is named 'close reference point' (CRP) and the distant reference point of the natural *Posidonia* meadow located 700 m from the transplanted zone is named 'distant reference point' (DRP) (Fig. 1). A fourth station located at the lower depth limit of the distant reference point of the natural meadow (DRP-LL) was added for the monitoring of carbohydrate reserves (see Section 2.6.3).

2.6.1. Environmental parameters

***Light Measurement.** A major cause of seagrass loss globally is the reduction of available sunlight for seagrass photosynthesis, which is the primary driver of seagrass growth (Duarte, 1991; Dennison et al., 1993; Duarte et al., 2005; Collier et al., 2016). To follow this parameter, HOBO data loggers (Pendant UA Temp/Light) were installed at the three stations (Transplants, CRP and DRP) 50 cm above the seafloor and light intensity was recorded every 10 min for all the duration of the construction works.

***Sediment chemistry.** Seagrasses are known to be able to release oxygen in sediments through their roots to create a small oxic zone (Pedersen et al., 1998). This function could be suppressed by reducing the photosynthetic process. If the sediment becomes anoxic, hydrogen sulfide levels above 10 μM could represent a lethal threshold (Calleja et al., 2007). Sediment chemistry was therefore studied through measurements of oxygen (O_2) and hydrogen sulfide (H_2S) in interstitial pore water. At each site, the sediment pore water was sampled in triplicates, by scuba diving, using syringes inserted at a depth of 10 cm in the sediment. After sampling, the syringes were stored in shadow and kept in an icebox at a low temperature. Back to the laboratory, water samples were treated according to the chemical analyses required. O_2 concentration was obtained using an iodine titration with thiosulfate according to the method of Winkler (Oudot et al., 1988) with an automatized system for small sampling volumes adapted by R. Biondo, (Laboratory of Oceanology-University of Liège). The probe (a Metrohm 6.0451.100 for redox titrations) is linked to a multimeter Fluke®. The software allows the remote manipulation via a computer of the Metrohm 655 Dosimat device and the automatization of the oxygen concentration measurement. It integrates the precise volume of each BOD, the lab and in situ temperature as well as the sample salinity. H_2S concentration was measured with a silver/sulfide ISM-146 FTH 25-XS electrode, coupled with a Sulfide Anti-Oxydant Buffer (SAOB) solution. For detailed protocols of the measure of O_2 and H_2S, see Abadie et al. (2016).

2.6.2. Structural parameters

***Photogrammetry.** Underwater photogrammetry defines the three-

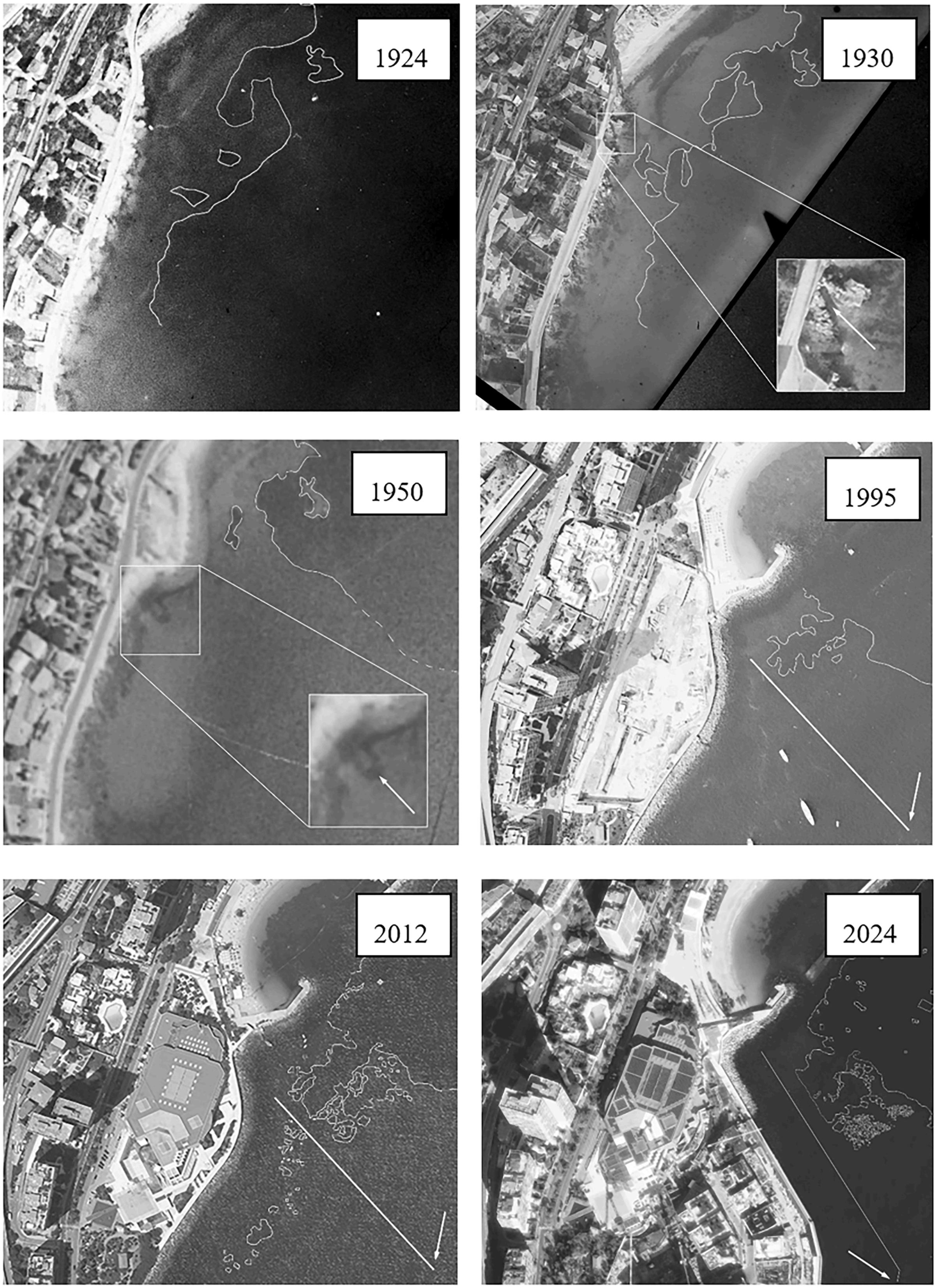

Fig. 2. A century of evolution of the shore in Monaco. In 1924, the upper limit of the *Posidonia* seagrass is continuous and parallel to the coast. In 1930, channeling and discharge of rainwater onto the shore. In 1950, extensive regression of the *Posidonia* seabed is observed, building of a first polder. 1995, discharge of rainwater in the open sea with a 295 m long outfall and slight progression of the seagrass to the west despite a massive artificialisation of the coast. In 2012, progression of the meadow to the west. In 2024, after the construction of the Mareterra platform. *Posidonia* meadows situated in the workshop area has been partially relocated close to the natural seabed situated to the east of the outfall, in the Larvotto MPA.

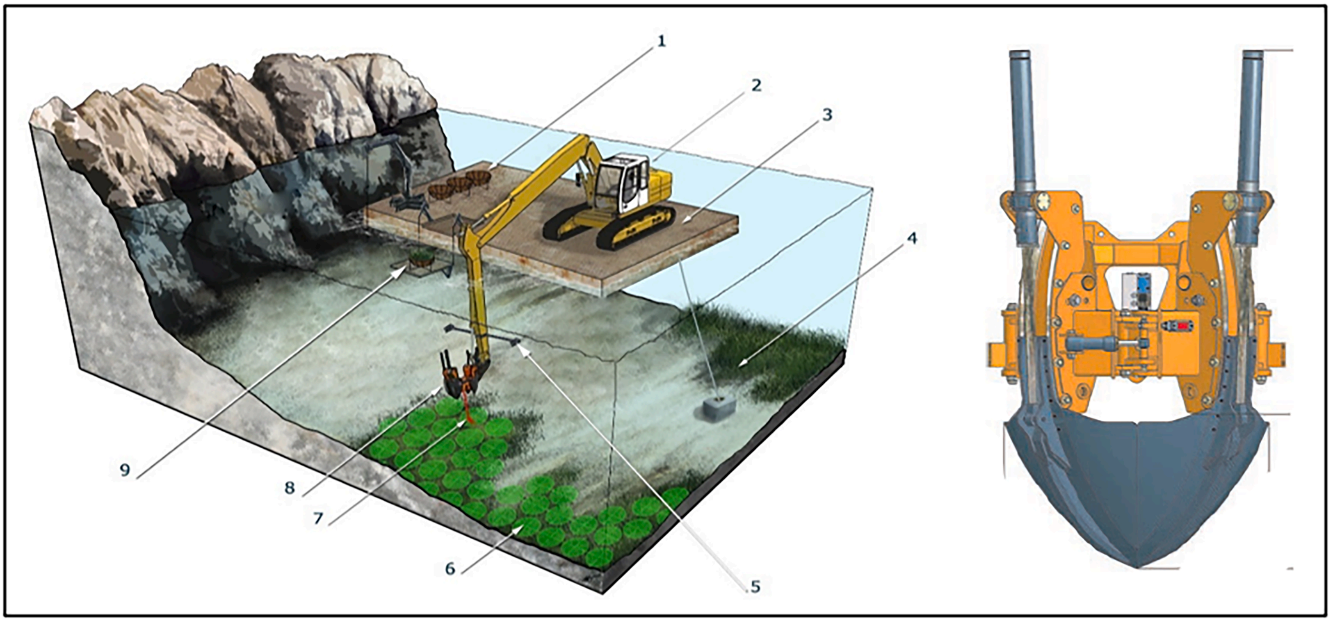

Fig. 3. Removal platform and Optimal tree spade transplanter 880. Transport baskets (1), long-arm excavator (2), Jack-up platform (3), platform anchoring lest (4), control cameras (5), expected sods with targets (6), laser pointer (7), transplanting machine (8), baskets lift (9).

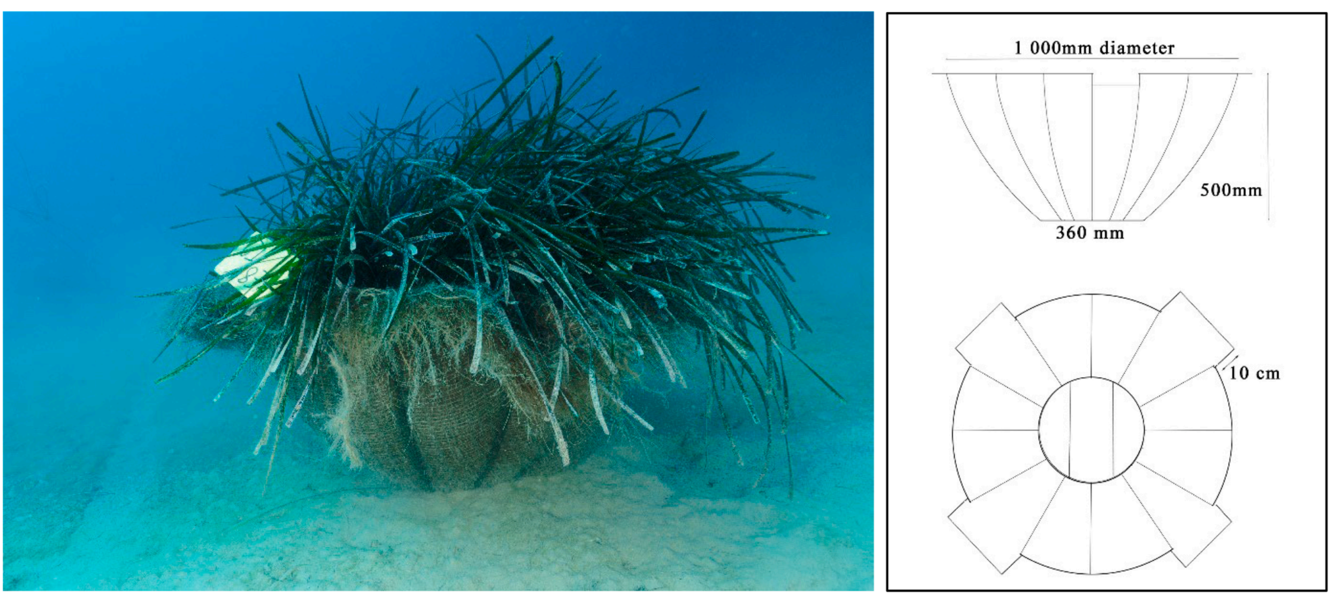

Fig. 4. Iron and coco fiber transport basket.

dimensional (3D) reconstruction of a seafloor, using a high number of images taken from different perspectives (Figueira et al., 2015). Besides 3D reconstructions, this technique also allows producing orthomosaics of survey areas with a high resolution (mm to cm) and high reconstruction accuracy (Marre et al., 2019). Photogrammetry has seen increasing application in the field of marine ecology and has notably been deemed suitable for monitoring seagrass cover using orthomosaics (Mizuno et al., 2016; Marre et al., 2020). In this study, photogrammetry was used to assess the total living seagrass area, an analysis which was repeated annually.

From 2017 to 2023, all photogrammetric acquisitions were conducted once a year at the same period of time, in September or October, to avoid differences in leaf growth stage. The photographs were taken by one scuba diver using a 16 Mega Pixel Nikon D4 in a waterproof Seacam housing, mounted with a Nikon RS 20 - 35 mm lens (set to 20 mm). For each acquisition, the diver swam approximately 2.5 m above the seafloor, conducting parallel, regularly spaced transects at a speed of 20 - 25 m.min^{-1}, with a time lapse of 1 second between pictures. To achieve a satisfying balance between depth of field, exposure and sharpness, camera settings were adjusted before each acquisition in accordance with the environmental conditions (lighting conditions and visibility). Shutter speed was consistently set to 1 / 250 s in order to avoid image blurring, and aperture and sensibility were adjusted accordingly (F11–16, ISO 1200–4000 among all datasets). Focus was set automatically before each acquisition, then turned to manual. This protocol allows reaching a precision of 0.3 mm / m from the model center in XY and 1.2 mm / m in Z (precision in Z has no impact as mapping is performed in two dimensions) (Marre et al., 2019).

All photogrammetric datasets included between 2995 and 5792 images and were processed with Agisoft Metashape Professional Edition

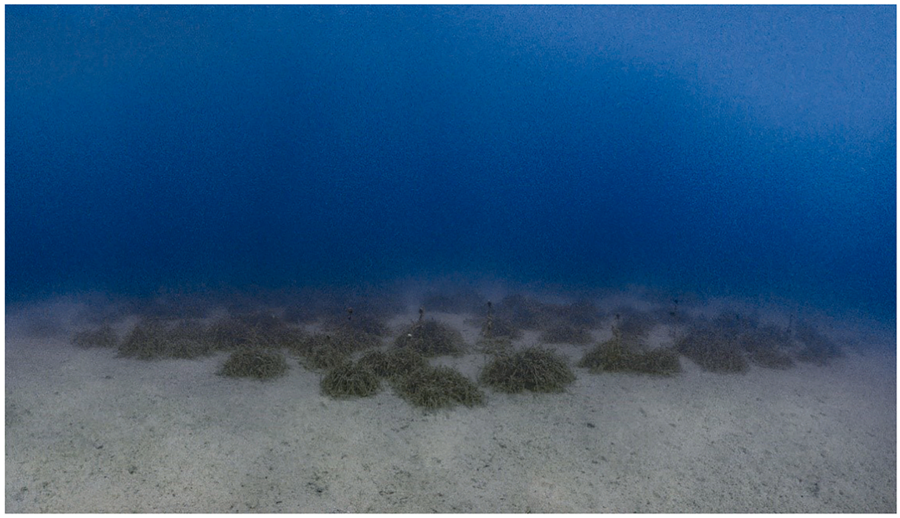

Fig. 5. Transplants in Larvotto in July 2024.

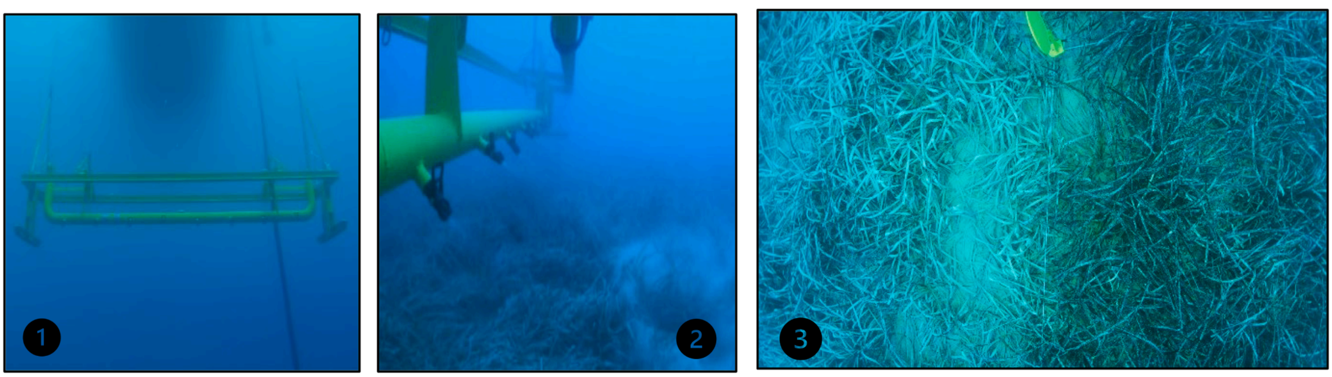

Fig. 6. Cleaning machine (1), water jets (2), efficiency (3). Left part and right part: before and after cleaning operation, respectively.

V. 1.8.4. This commercial software is widely used by the scientific community (Burns et al., 2016; Casella et al., 2017) and uses a classic photogrammetric workflow.

The parametrization of the different photogrammetric steps was set as follows : (1) Bundle adjustment: high quality (original image resolution); key point limit = 60,000 (maximum number of feature points detected on every image); no tie point limit (no upper limit for the number of associated tie points between images); generic preselection enabled (first pass using lower accuracy setting prior to the high-quality adjustment, to save processing time); (2) Optimization (adjustment of estimated point coordinates and camera parameters minimizing the sum of reprojection error): f (focal length), cx – cy (principal point offset), b1 – b2 (affinity and non-orthogonality coefficients), k1 – k2 – k3 – k4 (radial distortion coefficients) and p1-p2 (tangential distortion coefficients); (3) Dense cloud: low quality (original image resolution downscaled by factor 8); (4) Mesh: high quality (original image resolution) / surface type = arbitrary (any kind of object); (5) Orthomosaïc: export resolution = 0.003 m.

The first model (2017) was orientated and scaled using four coded markers fixed on a 0.9 × 0.9 m cross-scale bar placed within the mapped area and used as a reference to manually align all other models together using common ground control points located all over the mapped area. Once all models were aligned, all orthomosaics were produced and exported using the same local metric coordinate system. Using QGIS Desktop 3.22, all seagrass patches were manually digitised to assess the total living seagrass area once a year.

***Shoot abundance.** The abundance of shoots (the number of *P. oceanica* shoots in a basket) was determined annually in 30 transplanted baskets until 2024. Abundance is more appropriate than shoot density for studying the survival of transplants in the first years because the seagrass can extend its surface without increasing its density. Given the non-normality of the data (Shapiro test, p-value < 0.05), non-parametric tests were performed to assess statistical differences of shoot abundance over time.

2.6.3. *Physiological parameters*

***Total carbohydrate reserves in rhizomes.** Carbohydrates are stored in the rhizomes between September and June and provide the essential energy for the plant growth (Pirc, 1989). Mobilisation of reserves enables overwintering and regrowth in spring (Alcoverro et al., 2001). A fourth station located at the lower depth limit of the distant reference point of the natural meadow (DRP-LL) was added for the monitoring of this parameter. DRP-LL was considered as the minimum reference value to be maintained in the rhizomes of the transplants in April-May and September to guarantee their survival (Govers et al., 2015). The samples were collected at the four stations (Transplants, CRP, DRP, and DRP-LL) by scuba divers. This sampling was performed every month between December 2017 and December 2019, and then every year until September 2022. Fresh pooled samples were stored at −20 °C and sent to MicroPolluants Technology SA (Saint Julien Les Metz, France where soluble carbohydrates and starch (TNC) were extracted from the ground dry tissues in hot (80 °C) ethanol and analysed using the methods described in Alcoverro et al.(1999).

3. Results

3.1. Transplantation speed

The transplantation of 384 m^2 was performed in 24 days. The average speed was 18.4 transplanted baskets per day (i.e. 14.7 m^2 / day) with a maximum of 41 baskets/day (i.e. 32.8 m^2 / day). The main slowing factors were bad weather (swell in excess of 0.8 m) and the need to carefully move the self-elevating platform to avoid damaging the seagrass to be removed.

3.2. Structural integrity of the transplants

Each basket was quality controlled at the time of collection, after transport and after planting. The transplant unit taken had to have more than 50 % coverage, be roughly horizontal and have less than 8 cm of rhizome baring. Twenty transplants were deemed non-compliant and therefore replaced. Thirty-five percent of the baskets had an estimated coverage of 50–70 %, sixty percent of the baskets had an estimated coverage of 70–90 % and five percent of the tranplant units had 100 % coverage. In this respect, the quality objective was exceeded. In the Eastern part of the collection site, the very fine and muddy sediment tended to flow away when the transplanter opened while the *Posidonia* transplants were still held by the spades. This caused many tranplant units to be bared over heights of about 5 to 8 cm. To correct this, 20 cm metal staples were placed by divers to make sure the rhizomes stayed on the seabed.

3.3. Light measurement

The Kruskall-Wallis test showed that there was no difference in the amount of light measured between Transplants & CRP (p-value = 0.2), but that Transplants and CRP received less light than DRP over three years (respectively, p-value = 0.001 & p-value =0.02).

3.4. Shoot abundance

A significant decrease in densities was observed in the first three years (Kruskal-Wallis; p-value < 0.001), followed by a significant increase (Kruskal-Wallis; p-value < 0.01), reaching a value in 2024 similar to that measured in 2017 (Kruskal-Wallis test; p-value > 0.05). Although the number of shoots per basket was relatively homogeneous in 2017 (82.7 shoots / basket ± 25.6 SD), the dispersion of the data increased and became much greater over time (115.5 shoots / basket ± 83.8 SD in 2024) (Fig. 8).

3.5. Total carbohydrate reserves in rhizomes

The monthly results from December 2017 to August 2019 showed a classic seasonal cycle, with minimum carbohydrate levels in late winter, an increase in spring, and maximum concentrations in late summer at all stations (Fig. 9). Low values were measured in March 2018 and March 2019 but above the minimum threshold (based on the value of DRP-LL) guaranteeing the survival of the meadow.

3.6. Sediment chemistry

In 2017, H_2S levels were below the lethal threshold (10 μM) at all sites. In 2018, H_2S levels above the lethal threshold (10 μM) were observed in almost half of transplants. In 2019, there was a general improvement, with a reduction in the number of measurements above the lethal threshold, and by September 2020, all sites had hydrogen sulfide levels below the lethal threshold.

The opposite trend was observed for O_2: the oxygen saturation of the sediment pore water in transplants was highest in May 2017 (83.14 %, DRP value = 49.47 %) and decreased drastically in September 2017 (13.42 %, DRP value = 128.68 %). The saturation then gradually increased, reaching 20.79 % in April 2021 (DRP value = 33.11 %).

3.7. Survival, vegetative growth, and sexual reproduction of transplants

After two years of decline in 2018 (−21.6 %) and especially in 2019 (−39.2 %), the covered area started to increase again in 2020 (+12 %) after the end of the construction work; the annual increase in cover was then 23.9 % in 2021, 9.8 % in 2022, 11.1 % in 2023 and 25.8 % in 2024 (Fig. 10).

In the transplanted area, the meadow lost 201 m^2 in the first two years before recolonising 207 m^2 over the next five years. Orthomosaïcs showed that the changes in the surface area covered by the transplants were not homogeneous and were the fastest in the central part of the transplant area, in the shallowest zone (Fig. 11).

During the winter of 2019–2020 and the following spring, simultaneous flowering was observed in both the transplanted seagrass beds and the adjacent natural *Posidonia* meadow in Larvotto (CRP) (Fig. 12).

4. Discussion

To our knowledge, this case study on seagrass transplantation is one of the few approaches to the mechanical restoration of seagrass beds on an industrial scale ever tested anywhere in the world, and a first success for *P. oceanica* given the large surface area involved (384 m^2 to be transplanted in a very short time frame). The combined efforts of academic knowledge, financial resources, and technical innovation enabled the transplantation to be carried out in a timeframe compatible with a major infrastructure project.

The results, documented over a period of eight years (2017–2024), demonstrate the positive dynamics of the transplanted seagrass meadow, which has resisted the transplantation and the impact of the intensive marine construction works going on nearby. This long-term monitoring project shows that the sod-transplanted meadow rapidly developed structural and functional characteristics fully comparable to those of nearby natural meadows. The fact that *P. oceanica* transplants flowered three years after the operation - a rare phenomenon, occurring only four times in the last 20 years in Monaco (2003, 2006, 2009, 2015) - suggests that some transplants had the carbohydrates reserves needed to develop inflorescences and produce seeds. This level of energy reserve may have been difficult to achieve for the transplants (Calvo et al., 2006; Gobert et al., 2005a, 2005b). Some mortality occurred, especially during the first years of the project, essentially due to the uprooting of rhizomes during strong winter storms (Adrian storm in October 2018 & Alex storm in October 2020) but also due to the high levels of sedimentation and the reduced luminosity caused by marine works that continued for two years after transplantation (Fig. 7). The increase in the dispersion of density data across baskets over time is due to a clear divergence between baskets that held up well from 2017 to 2019 and have grown rapidly since 2020, and those that were deteriorated severely in the early years. Although it is not possible to distinguish between the relative importance of storms and construction impacts, it is important to note that transplanted plants survived particularly harsh conditions during the first two years with reduced light input and high levels of sedimentation. The effects of the reduction in light at macro and micro-scale have been already described (Erftemeijer and Lewis, 2006; Lee and Dunton, 1997). In our case, low levels of carbohydrates were measured in the rhizomes in spring 2018 and 2019 (during the maximum intensity period of marine work in the Mareterra project) at stations close to the construction site where turbidity was the highest. Until 2019, when the most turbidity-inducing works were completed, the carbohydrate content increased at all stations to exceed that of 2018. Another slight decrease was again observed in September 2020, probably due to the growth of seagrass at all stations, which mobilised the resources allocated to the rhizomes (Scartazza et al., 2017). Low concentrations in O_2 and high concentrations in H_2S were also observed during the first years in the

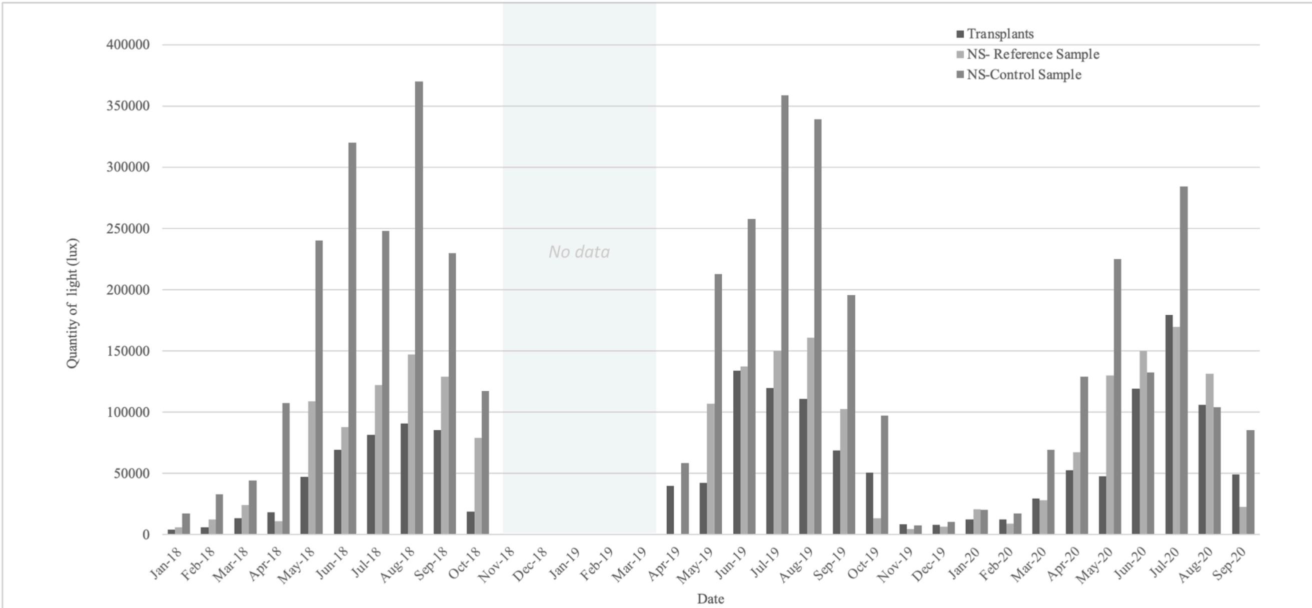

Fig. 7. Quantity of light (lux), from January 2018 to September 2020, received by sensors at three stations. (i) sensor in the Transplants, (ii) sensor in the Natural Seagrass *Posidonia oceanica* as a Reference Sensor (closed to the construction site).

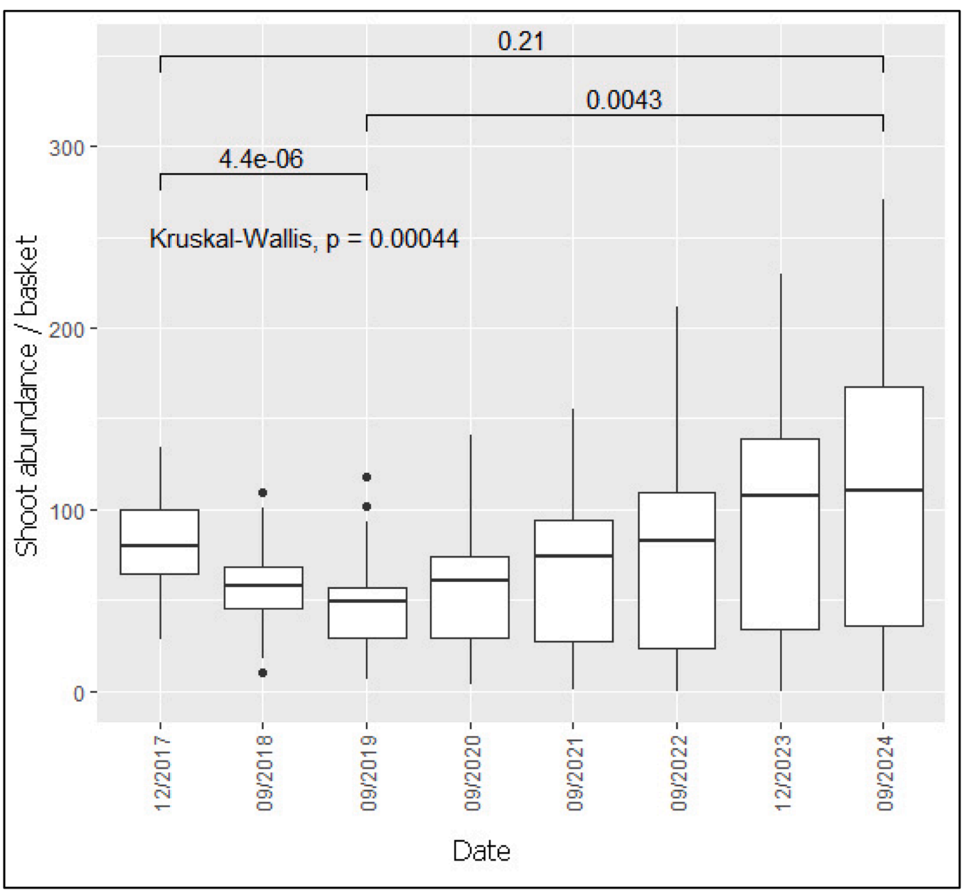

Fig. 8. Abundance of *P. oceanica* shoots in 30 transplanted baskets from 2017 to 2024 in Monaco. The brackets show the different periods used to compare the shoot abundance over time, using Kruskall-Wallis test. The numbers are the p-values associated to each period.

transplanted area, related to this light reduction and then to the reduction in photosynthetic activity. This process is similar, to a lesser extent, to what has already been observed in impacted meadows near aquaculture farms or in the vicinity of anchor marks (Abadie et al., 2016; Apostolaki et al., 2011).

The transplantation by sods showed many advantages for the plants,

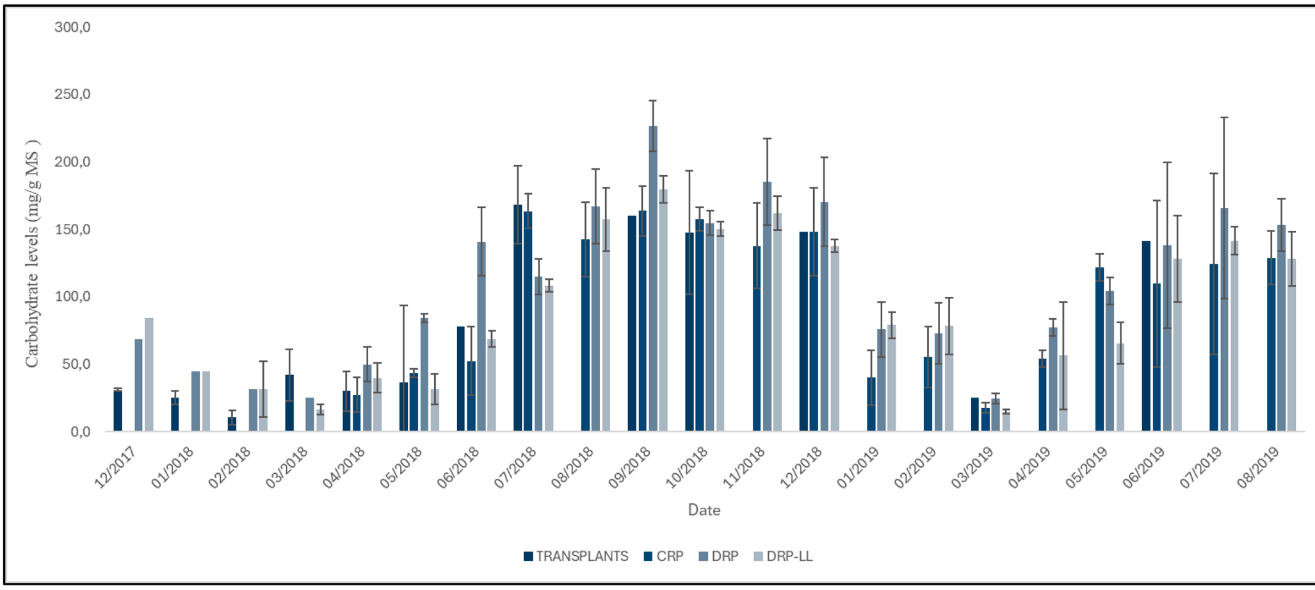

Fig. 9. Variation in TCR (total carbohydrate reserve) in Posidonia oceanica rhizomes at four stations: Transplants in Larvotto, close reference point 'CRP', distant reference point 'DRP', distant reference point in the lower limit 'DRP-LL'.

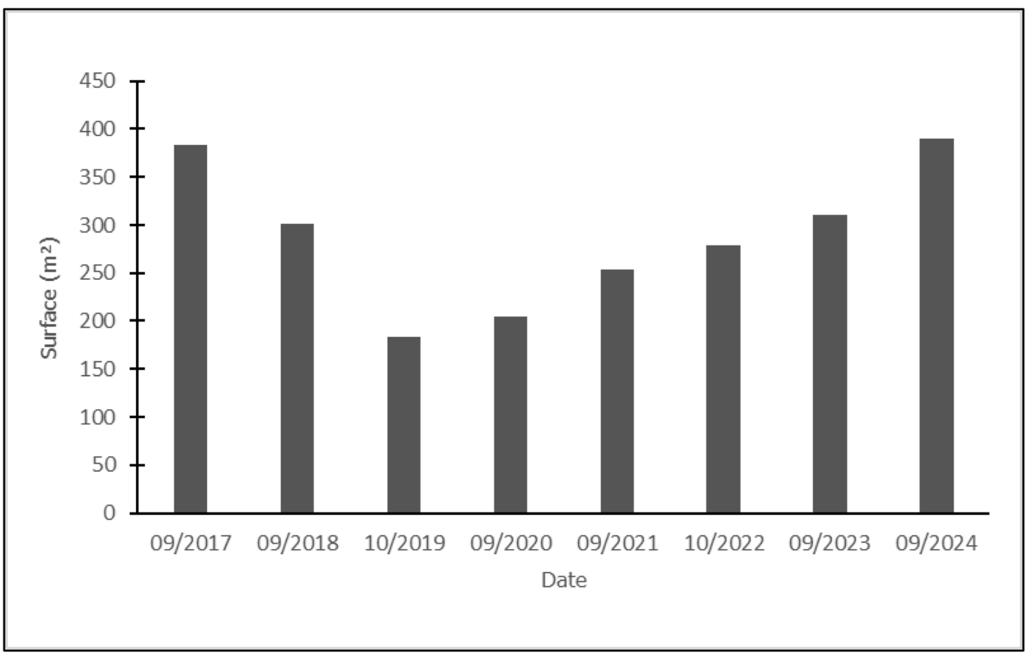

Fig. 10. Temporal evolution of the combined total surface area covered by transplants (aggregated) in Larvotto between 2017 and 2024.

compared to cuttings transplantation, and certainly helped them to survive: preservation of networks of long rhizomes with their large amounts of mobilizable carbohydrates reserves (Govers et al., 2015), better resistance to root damage as roots are already fixed in the sediment (Fonseca et al., 2008), oxygenation of the sediment through the roots network and prevention of the formation of toxic sulfides (Marbà et al., 1996), conservation of the associated fungi (Panno et al., 2013) and bacteria which are in a symbiotic relationship with the seagrasses, converting pure nitrogen (N_2) into substances that the plants can use in order to thrive (Mohr et al., 2021), large patches that are more likely to succeed in stabilizing sediments and overcoming stochastic environmental stress (Carr et al., 2010). Indeed, the latter beneficial effect is particularly observed through the analysis of orthomosaics, which shows that the recolonization of empty spaces between the baskets occurs more quickly in the center of the transplantation area than at the edges (Fig. 11). Since it is a sod transplantation, conserving most of the initial density present in the *Posidonia* meadow before it was transplanted, and because the baskets were placed close together, self-facilitative processes, such as the mutualistic sheltering effect, may have enhanced the recolonization of the bare area between the baskets and contributed to the overall health and development of the transplants (Valdez et al., 2020; Vidondo et al., 1997). During "classic" transplantation with seagrass fragments of a rhizome with a couple of shoots, P. oceanica use its reserves to produce a network of roots and plagiotropic rhizomes for stable anchorage in the sediment and substrate colonisation. This occurs at the expense of leaf production, with foliar nitrogen and phosphorus being translocated to the underground parts. Concentrations of N and P can decrease by nearly 30 % due to the

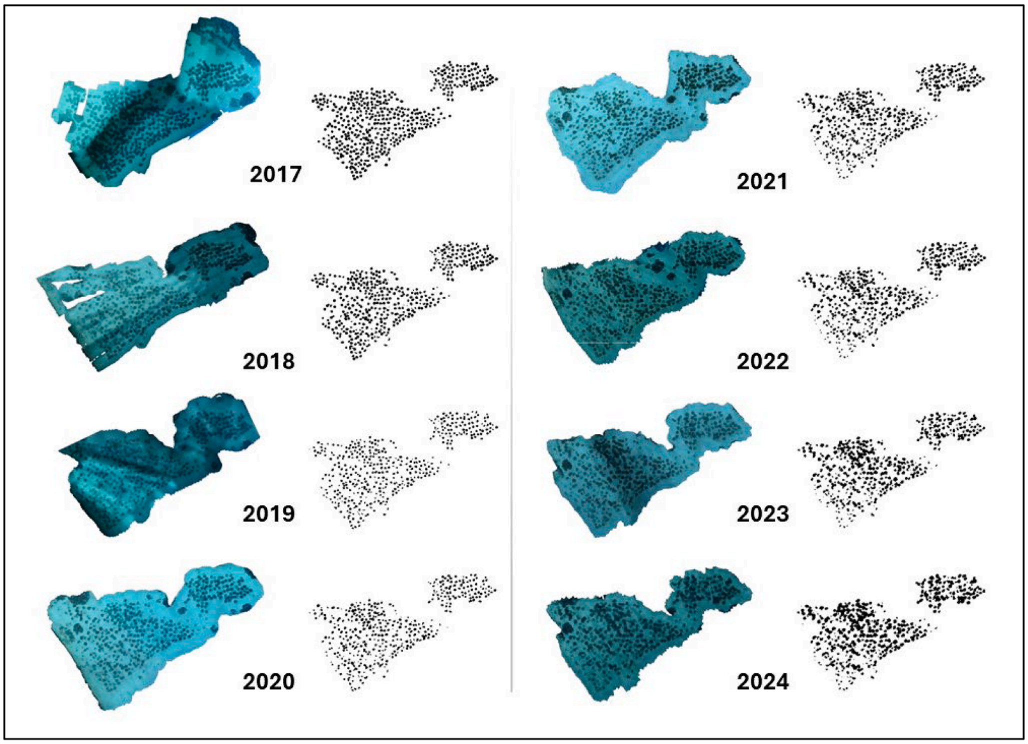

Fig. 11. Orthomosaïcs and surface projections of the transplanted seagrass meadow realised in September or October, from 2017 to 2024. The orthomosaics were built from acquisitions of 2995 to 6986 images.

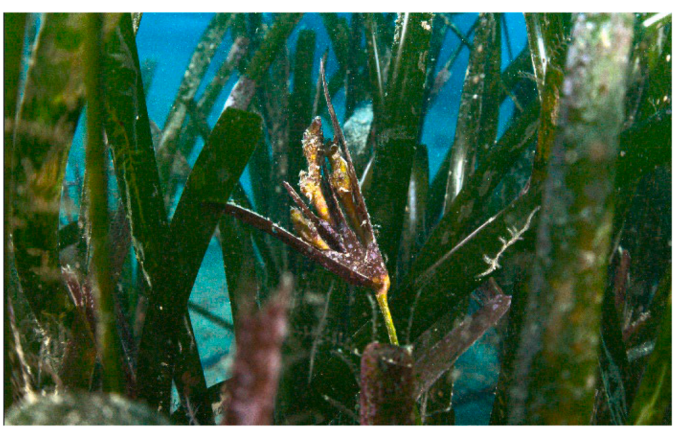

Fig. 12. Flower in the transplanted meadow in March 2021.

inability of the plant to uptake nutrients from the sediment. Natural seasonal variations in N and P in tissues disappear, and the plant fails to replenish its reserves during at least three years (Gobert et al., 2005a; Lepoint et al., 2004). This 'post-transplant shock' did not occur in our study, due to the sod transplantation technique used and despite the impact of the site work that caused increased turbidity for two years.

Although some seagrass sod transplantation projects are described with a much larger cover area [e.g., 2 250 m^2 in (Curiel et al., 2021)] than the area covered in our study (i.e., 384 m^2), these studies collected and transplanted the sods in very shallow waters (maximum depth of 5 m), which facilitated the technical aspects and speed of transplantation. To our knowledge, this study is among the first to harvest sods and transplant them in deep waters (15–20 m), demonstrating the potential of applying this newly developed technique to seagrass meadows thriving at depths beyond a few meters. Moreover, this case study also highlights the value of post-transplantation corrective work, which probably also supported the resilience of our plants. This involved fixing loose rhizomes, adjusting the level of baskets, and cleaning leaves during periods of heavy sedimentation due to construction work. It seems important to anticipate the necessity of such operations in terms of budget, human, and technical resources, as it represented 15 % of the total budget of the operation. Previous studies on seagrass sod transplantation have primarily focused either on rescuing seagrass meadows threatened by marine construction activities, such as dredging or port expansions (Bedini et al., 2020), or on restoration efforts by transplanting sods from a donor site to a degraded site (Curiel et al., 2021; Suykerbuyk et al., 2016). Our study stands out from previous work, as the transplantation design not only facilitated the rescue of the seagrass meadow affected by construction activities but also contributed to restoring the lower depth limit of the seagrass meadow in the Larvotto Marine Reserve, which had been severely degraded in the past. It would have taken at least 400 years for the meadow to naturally recolonize the transplantation area (28 m wide), given its natural horizontal slow growth rate of 1 to 6 cm/year/apex (Marbà et al., 1996). Thanks to the ecological restoration, with a distance between transplants reduced to a maximum of 2–3 m, it is hoped that the area will be fully recolonized within about 15–20 years without any further human intervention.

Transplantation of seagrass meadow as a tool to avoid destruction in the case of coastal construction projects has long aroused strong reservations among scientists (Boudouresque et al., 2021; Bradley et al., 2022; Sánchez-Lizaso et al., 2009). This thinking has strongly encouraged the authorities to limit experiments in active *P. oceanica* restoration. As a consequence, the development of real operational techniques stagnated for several decades (Pansini et al., 2022) and delayed innovations. Serious experiments were few, carried out on a very small scale and without a clear strategy (Bellan Santini, Lacaze, et Poizat 1994). At the same time, many coastal projects, such as the construction of ports and dams, installation of cables and pipes, were approved despite their impact on seagrass beds because they were recognised as being of major socioeconomic importance. In such cases, the destruction of seagrass meadows at best opened a process of ecological compensation, often based on the immersion of artificial reefs, without transplantation being envisaged as a viable impact-reduction measure. This is the case in this typical statement of the environmental French authority concerning the extension of the port of Solenzera in December 2016: 'In order to compensate the destruction of 3 000 m^2 *Posidonia* meadows inside the new port enclosure, habitat reefs will be installed in the southern protection structure' (Environmental authority, 2016).

From our point of view the use of transplantation to save a seagrass meadow destined to be destroyed is legitimate and totally ethical. Transplantation allows a concrete reduction in impact and, if carried out using the sod methodology described in this paper, the preservation of an architectural species with all its associated flora and fauna, including the seabed. There are several examples of regulatory requirements for translocation of protected plants worldwide in association with construction or development projects. However, these mitigation projects rarely achieve the intended 'no net loss' of protected species due to issues with timelines and procedures or high levels of mortality of the translocated individuals. Such projects are often process driven, focusing more on meeting legislative requirements which enable the development to proceed, rather than meaningful attempts to minimise the ecological impact of developments and demonstrate conservation outcomes (Doyle 2023). In the case of *P. oceanica*, transplantation is, for the moment, not even recognized as a relevant impact mitigation measure but only accepted as an additional and voluntary measure outside any regulatory framework (Pergent Martini et al., 2024). In this logic, developers are not encouraged to commit a substantial budget to a transplantation measure but are sadly encouraged to request authorisation for the destruction of a protected species, with pseudo-compensation for the net loss of biodiversity by artificial fish reefs, rather than considering safeguard measures through transplantation.

This work, carried out on an emblematic species, at significative depth, provides a solid argument in favour of transplantation, which is a real solution for avoiding the destruction of seagrass meadow. Sod transplantation poses technical challenges, requires a suitable reception area, and carries a risk of failure. Transplantation is also expensive, in our case the budget of around 325€/m^2/year including post-operation cares and scientific survey was borne by the private project owners. This budget is consistent with the order of magnitude of the values reported by Bayraktarov (190$/$m^2$/year) for shallower seagrasses transplantations performed in developed countries (Bayraktarov et al., 2016). Nevertheless, this expense remains low given the cost of many coastal construction projects around the world. For example, in our case, the cost of the transplant represented only 0.05 % of the total construction project budget.

Despite uncertainties, mitigation translocations do represent an opportunity to generate genuine conservation gains if objectives, resources, timelines, and funding align with conservation outcomes (Doyle et al., 2023). That is why, to our point of view, seagrass transplantation should be favored as a mitigation measure, not only to meet legislative requirements which enable the development to proceed but to align with the objectives of biodiversity no net loss and adhere to the mitigation hierarchy (Cares et al., 2023). If feasible, transplantation should be given priority over any compensation measures.

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CRediT authorship contribution statement

Descamp Pierre: Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Personnic Sébastien:** Investigation, Formal analysis. **Gobert Sylvie:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Boulenger Arnaud:** Writing – original draft, Formal analysis. **Leduc Michèle:** Funding acquisition, Formal analysis. **Delaruelle Gwenaelle:** Investigation, Data curation. **Barroil Adèle:** Formal analysis. **Marre Guilhem:** Writing – original draft, Investigation, Formal analysis. **Holon Florian:** Investigation. **Deter Julie:** Writing – original draft, Methodology, Investigation, 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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Data availability

The data that supports the findings of this study are available from the corresponding author, Pierre DESCAMP, upon reasonable request.

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