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Transplantation of seagrass (*Zostera noltei*) as a potential nature-based solution for the restoration of historically contaminated mudflats

Vítor H. Oliveira [a,*], B.A. Fonte [a], A.I. Sousa [a], D. Crespo [b,d], J.M. Dias [c], N. Vaz [c], D. Matos [d], E. Figueira [d], M.E. Pereira [e], A.I. Lillebø [a], M. Dolbeth [b], J.P. Coelho [a]

[a] *ECOMARE, CESAM - Centre for Environmental and Marine Studies, Department of Biology, University of Aveiro, Estrada do Porto de Pesca Costeira, 3830-565 Gafanha da Nazaré, Portugal*

[b] *CIIMAR - Interdisciplinary Centre of Marine and Environmental Research, Novo Edifício Do Terminal de Cruzeiros Do Porto de Leixões, Avenida General Norton de Matos S/N, 4450-208 Matosinhos, Portugal*

[c] *CESAM - Centre for Environmental and Marine Studies, Physics Department, University of Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal*

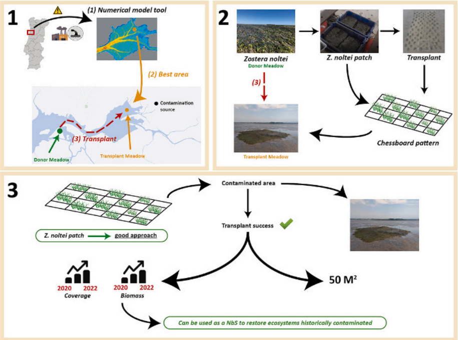
[d] *CESAM - Centre for Environmental and Marine Studies, Department of Biology, University of Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal*

[e] *LAQV-REQUIMTE, Department of Chemistry, University of Aveiro, Campus de Santiago, 3810-193 Aveiro, Portugal*

HIGHLIGHTS

- *Zostera noltei* transplant into historically contaminated area was a success.
- In-situ transplant formed a compact meadow after two years.
- Use of *Z. noltei* patches in contaminated areas is a good approach.
- Numerical models are an essential tool in rehabilitation processes.

GRAPHICAL ABSTRACT



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ABSTRACT

Within the UN Decade on Ecosystem Restoration (2021–2030) framework, a Nature-based Solution (NbS) using *Zostera noltei* transplants was tested to restore a historically contaminated intertidal area. In-situ transplantation relied on patches of seagrass and sediment from a Donor meadow and its evolution was monitored for two years. The evaluation of the transplant success encompassed the seagrass coverage area, seagrass biomass, tissue mercury (Hg) accumulation, and photosynthetic efficiency.

The transplant was successful, with gradual increases in the coverage area in the target area indicating adaptation to local conditions already after the first year. Although some significant differences were observed in biomass and tissue Hg concentration over time, the similar translocation factors suggest the plant has effective defensive mechanisms to prevent accumulation and cellular damage. Additionally, the normal seasonal pattern

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* Corresponding author.
E-mail address: vitor.hugo.oliveira@ua.pt (V.H. Oliveira).

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of photosynthetic parameters indicates that contamination is not impeding its photosynthetic performance and growth, suggesting this NbS as a viable restoration strategy.

1. Introduction

Coastal lagoons are increasingly recognized for their significant ecological contributions. These transitional systems can host plants that regulate the climate by sequestering atmospheric carbon (Macreadie et al., 2019; Sousa et al., 2019) and can help to stabilize the sediment by increasing sedimentation rates (Barcelona et al., 2023), reduce the current velocity and energy (Perillo and Piccolo, 2021), and lower the risk of flooding by reducing the duration of surge and wave height (Infantes et al., 2022). These habitats also aid in controlling pollution and improving water quality by mediating the cycling of nutrients and the settling of suspending matter on the sediment (de los Santos et al., 2021; Oreska et al., 2021). Moreover, they serve as vital nurseries for coastal biota, providing a safe habitat and feeding grounds for juvenile fish and macrofauna (Franzitta et al., 2021; Greenberg et al., 2014).

These estuaries and coastal lagoons also provide valuable ecosystem services acquired via several activities, namely fisheries, tourism, agriculture, aquaculture, mariculture, industry, and mining, and even via conservation and restoration of their habitats.

Despite their economic and ecological importance, transitional ecosystems have been increasingly impacted by environmental pollutants from various sources such as industrial, agricultural, and urban activities over the past two centuries (Ferreira et al., 2019). Blasco et al. (2016) report that metals, polychlorinated biphenyls (PCBs), polycyclic aromatic hydrocarbons (PAHs), and organochlorine pesticides (OCPs) are among the most abundant pollutants in estuaries and coastal lagoons. As a result of the current loss of marine biodiversity in several estuarine ecosystems due to pollution, political and legislative initiatives have been undertaken at the European and international levels towards restoring ecosystems to improve biodiversity, human livelihoods, and combat climate change. These initiatives include the Ramsar Convention on Wetlands, Integrated Coastal Zone Management (ICZM), Industrial Emissions Directive (IED), and the European Union Habitats Directive (Council Directive 92/43/EEC, 1992) and Water Framework Directive (Directive 2000/60/EC, 2000). More recently, laws and directives have been implemented to reverse habitat loss and degradation, restore ecosystems, and promote a sustainable use of marine resources, such as the United Nations Decade on Ecosystem Restoration (2021–2030), the new EU Nature Restoration Law, and the new global agenda “Transforming Our World: The 2030 Sustainable Development Agenda” (Buelow et al., 2022; Rezek et al., 2019). These initiatives have led to an increase of ecosystem restoration initiatives in Europe over recent decades (Oliveira et al., 2024).

Various methods have been employed for ecosystem restoration, including physical methods such as dredging treatments, chemical methods like solidification/stabilization treatments, and biological remediation techniques such as phytoextraction and phytostabilization (Duchesne et al., 2020; Li et al., 2019; Liu et al., 2018; Oliveira et al., 2024; Song et al., 2019). Among these methods, biological remediation stands out as an advantageous solution due to its cost-effective approach, environmentally friendly characteristics, efficient transformation of organic contaminants into harmless substances, and minimal impact on ecosystems (Oliveira et al., 2024). This is evident in its ability to eliminate the need for sediment excavation, prevent disturbances in navigation channels, and minimize effects on neighbouring ecosystems (Hamad et al., 2021; Karimi et al., 2022; Rostami and Azhdarpoor, 2019; Vishwakarma et al., 2020; Zhang et al., 2020). Furthermore, the use of plants, such as seagrasses, not only aids in the restoration of degraded ecosystems and promotes local biodiversity and productivity, but also contributes to mitigate global warming through the sequestration of atmospheric carbon in aquatic and vegetated habitats, known as blue carbon (Brown et al., 2021; Sousa et al., 2017, 2019).

Despite efforts to improve the health of transitional ecosystems, contaminants discharged in the mid-20th century, prior to the implementation of policies to ban their discharges to natural systems, are still present in many systems. Coroa de Boi Bay (Brazil) (da Rosa Quintana and Mirlean, 2019), San Diego Bay (USA) (Hayman et al., 2020), Jinzhou Bay (China) (Li et al., 2012), Zuari Estuary (India) (Cruz et al., 2020) and Ria de Aveiro lagoon (Portugal) (Oliveira et al., 2018) are examples of historically contaminated areas. In the specific case of the Ria de Aveiro lagoon (Portugal), contamination derives from decades of effluent discharges into Laranjo Bay, an inner area of the lagoon located near an industrial cluster, and was once considered one of the most Hg contaminated systems in Europe (Válega et al., 2008). This contamination has led to the degradation of habitats and a decline in both fauna and flora. While the system has been undergoing natural attenuation in the last 30 years, erosive processes have been identified that may potentially resuspend the contaminants buried in the sediments (Coelho et al., 2014), justifying active restoration actions.

In this study, we propose the restoration with the seagrass *Zostera noltei*, which historically occurred in the area, as a Nature-based Solution (NbS) to remediate the contaminated mudflat, a way to reduce resuspension and stabilize the sediment layers to promote natural attenuation, while increasing biodiversity and all associated ecosystem services. Seagrass resistance to local sediment contamination was tested beforehand, and plants were found to not be affected by sediment contamination, suggesting that recolonization with *Z. noltei* can be an effective restoration strategy for historically contaminated coastal areas (Fonte et al., 2023; Oliveira et al., 2024).

This study is a step further, aiming to evaluate the response of *Z. noltei* to in-situ transplantation through a pilot colonization experiment, and to verify if the seagrass can tolerate the existing conditions in the historically contaminated area and improve its ecological status.

To achieve the proposed overall goal, the following specific objectives were defined: 1) to perform a pilot transplant experiment in the contaminated area and monitor the evolution/coverage of the meadow over time; and 2) to evaluate the seagrass biomass growth, its tissue Hg accumulation and its photosynthetic performance, to validate the use of seagrass transplantation as a NbS for ecosystem restoration.

2. Methodology

2.1. Study area

The Ria de Aveiro is located on the northwestern Portuguese coast (Fig. 1A). This coastal lagoon has four main channels (Mira, São Jacinto, Ílhavo and Espinheiro) and four primary sources of freshwater discharge (Vouga, Antuã, Caster and Boco rivers). This lagoon system has an area of 83 km^2 at high tide and is characterized by narrow channels and extensive salt marsh areas. The Aveiro lagoon is a mesotidal system, where the tide propagates from the mouth to the innermost parts of the lagoon. The hydrodynamics is mainly due to the semidiurnal tides that have an amplitude of 2 m, with a minimum of 0.6 m (neap tides) and a maximum of 3.2 m (spring tides) (Dias et al., 2000). Strong winds can also influence this circulation in shallower channels (Pinheiro et al., 2020).

Due to its location, the Ria de Aveiro has witnessed significant urban and industrial development over the years, leading to environmental concerns related to direct and indirect discharges of domestic and industrial effluents into the lagoon. Following the implementation of the Water Framework Directive, a multi-municipality sanitation system

(MMSS) was implemented in Ria de Aveiro watershed in 2005, with significant reduction of the point source nutrient loads (Lopes et al., 2017). On the industry side, the greatest impact to this lagoon occurred in the second half of the 20th century (Oliveira et al., 2018), when industrial waste was periodically discharged into the 2 km^2 inner bay known as Laranjo Bay (Fig. 1B and C), where several metal(loid)s (e.g., As, Hg, among others elements) were deposited (Monterroso et al., 2003; Pereira et al., 1998; Ramalhosa et al., 2001). These discharges originated from the Estarreja industrial complex (Stoichev et al., 2020), and although effluents are no longer discharged, the contamination is still present in the surface layers of sediment (Oliveira et al., 2018).

2.2. Site selection

Transplant site selection was based on a previous mesocosm study regarding the resistance of seagrasses to transplantation (Fonte et al., 2023), hydrodynamic modelling and seagrass survey and mapping of the target area (2019) (Sousa et al. unpublished data; C-GRASS project) when a small (5 m^2) natural patch was identified.

Delft3D model suite (previously calibrated and validated by Pinheiro et al. (2020) was employed to predict emersion times (ET), current velocity (V), and maximum depth (MD) of the water column in Laranjo Bay (Fig. 1C) in five different areas (L1, L2, L3, L4 and L5). Observation points were implemented (black dots in Fig. 1C) to determine the best area for the seagrass transplant within the historically contaminated mudflat.

Three numerical simulations were conducted to evaluate the variation of selected parameters in Laranjo Bay under extreme flood, drought, and normal discharge scenarios, with the only variation being the fluvial discharge of the Antuã River (the river that most influences Laranjo Bay). To simulate these scenarios, freshwater inflow values derived from the time series predicted by the SWIM model (Krysanova et al., 2000) were used, since the rivers discharge is not currently monitored. The minimum, average, and maximum river discharge scenarios for the Antuã River were 2 m^3 s^{-1}, 31 m^3 s^{-1} and 86 m^3 s^{-1}, respectively.

2.3. Site characterization

The Donor meadow selection was based on the proximity to the target site, similar hydrodynamic conditions, and logistical feasibility. The Donor meadow, covering 7.5 ha (Fig. 1B — green dot), is situated 3 km downstream from the target site (predicted by the Delft3D model).

Before proceeding with the transplantation, physicochemical parameters (salinity, temperature and pH) were measured, and a characterization of the sediment (organic matter content, grain size distribution and metal(loid) concentrations) was conducted at both the Donor and Transplant sites. For this purpose, an exploratory field campaign was conducted, during which superficial (top 5-cm layer)

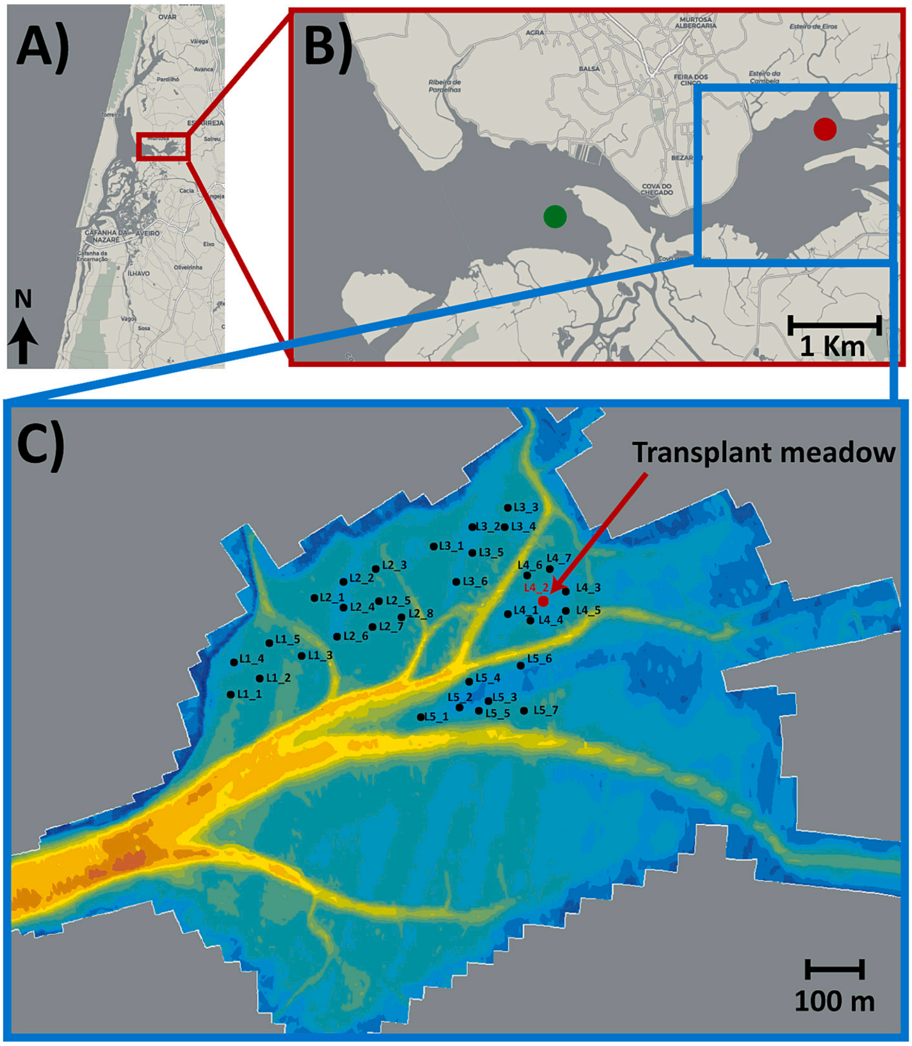

Fig. 1. Map of (A) the Ria de Aveiro coastal lagoon (Atlantic coast, Portugal), (B) study area and (C) observation points (represented by black dots) used in the Delft3D model in Laranjo Bay. Green and red dots in B) represent the Donor and Transplant meadow, respectively. Red dot in C) corresponds to the Transplant site.

sediment samples were collected in bags, and water parameters were measured. In the laboratory, the sediments were divided into two aliquots. One aliquot was freeze-dried, and subsamples were taken to analyse metal(loid) concentrations, including arsenic (As), cadmium (Cd), copper (Cu), mercury (Hg), nickel (Ni), lead (Pb), tin (Sn), titanium (Ti), uranium (U), and zinc (Zn). The other aliquot was dried, disaggregated and homogenized to analyse organic matter content and grain size.

Total Hg concentrations in the sediment samples were measured using a LECO AMA-254 Advanced Mercury Analyzer, following the methodology described by Oliveira et al. (2018). The analyzer's performance was verified daily through the analysis of Certified Reference Materials (CRMs) with similar matrices, both at the start and end of each day. The recovery rates for CRMs BCR-277R and BCR-143R were within their respective confidence intervals, ranging from 96 % to 112 % (n = 10) and 102 % to 108 % (n = 10), respectively. Each sample was analysed in triplicate, with the coefficient of variation consistently below 10 %.

For the quantification of other metal(loid)s, Inductively Coupled Plasma Mass Spectrometry (ICP-MS) Thermo X Series was employed. The sediment samples were processed according to the US EPA 3051 protocol. Similar to the Hg analysis, the performance of the ICP-MS was monitored daily. To ensure accuracy and reliability, parallel blank digestions and certified reference materials (ERM-CC141 and BCR-143R) were analysed to control for potential contamination. The recovery rates for these CRMs ranged from 100 % to 109 %.

The organic matter content was determined by loss on ignition (4 h at 500 °C), and the grain size analysis of the sediments was determined by wet sieving following the methodology described at Oliveira et al. (2018).

2.4. Transplant setup

The choice of transplant method was based on the results of Costa et al. (2022), which tested different seagrass transplantation and restoration methodologies. These methodologies included different anchoring methods (metal frames, nails, bamboo sticks), shoots inserted unanchored into the sediment, and intact units of sediment with seagrasses, referred to as a patch (or sod) of seagrass. Based on their research, the recommended transplant method is the use of a patch of seagrass, specifically in this case, a patch of *Z. noltei*. This technique allows the transfer of plants and sediment with seagrass, without any destruction of roots, rhizomes, leaves, and the rhizosphere.

The patches of *Z. noltei* were collected with the help of a shovel (patch area of 20 × 30 cm, ≈5 cm deep) and were transported by boat to the Transplant site. The collection of patches was done randomly and dispersed, to minimize the impact on the Donor meadow.

At the chosen Transplant site (Fig. 1B and C — red dot; and Fig. 2B), the patches of *Z. noltei* (n ≈ 220 per year) were placed in the sediment, levelled with the surrounding sediment, with the leaves pointing upwards. Transplants were placed in a chessboard pattern, alternating patches of seagrass and bare sediment (Fig. 2C), as previously tested and validated by Costa et al. (2022), to allow the expansion of *Z. noltei* in all directions.

Transplants were performed in the summer, to allow the seagrass to adapt to the new conditions and the patches to remain cohesive in the new site before the more challenging autumn and winter seasons, when periods of heavy rainfall and increased water flows may cause erosion.

The first transplant took place in late July 2020 (Fig. 2D), where an area of 25 m^2 was transplanted and the second transplant (expansion from 25 to 50 m^2, Fig. 2I) was carried out at the end of August 2021.

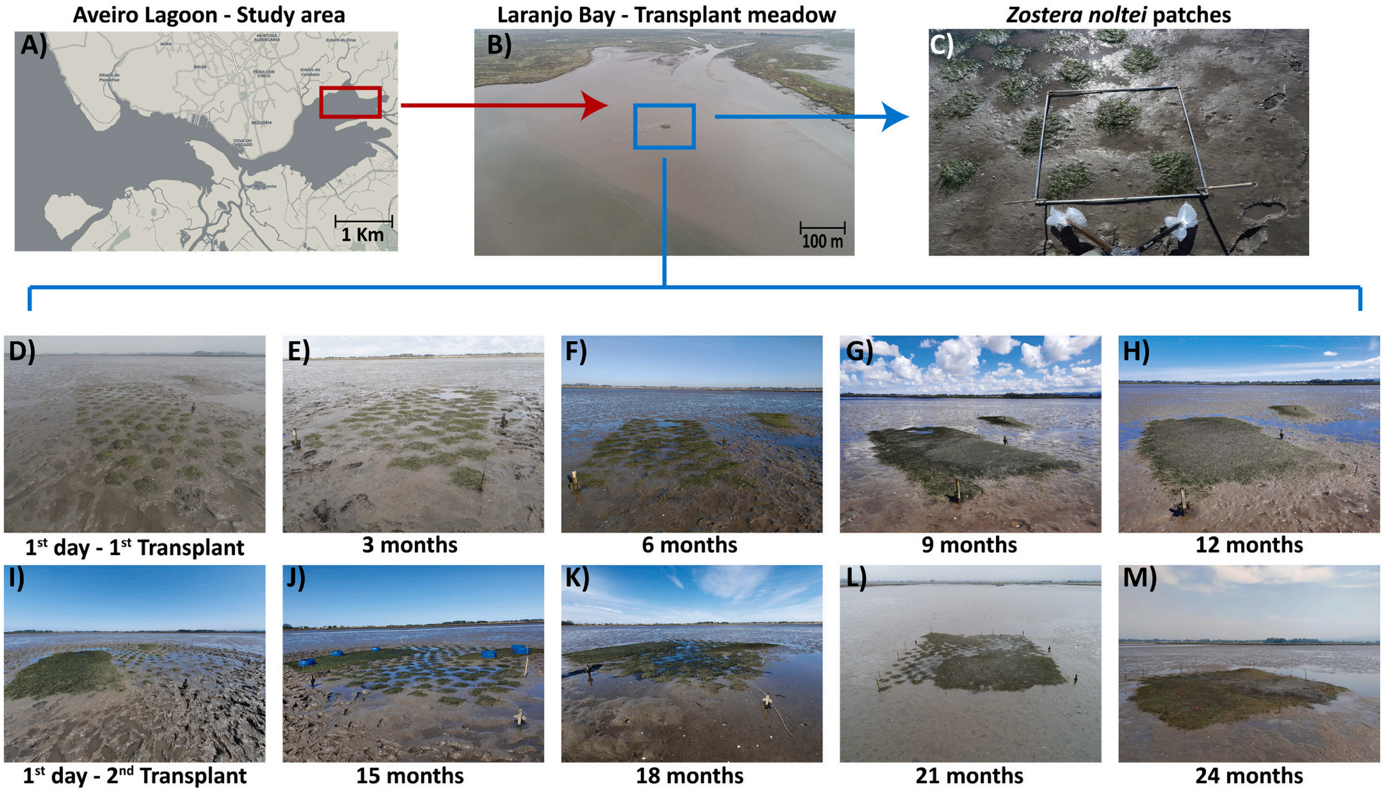

Fig. 2. Schematic plan of the Aveiro lagoon channel and Laranjo Bay (A), Transplant meadow in Laranjo Bay (B) and checkerboard pattern of seagrass transplants (C). Images from (D) to (M) illustrate the evolution of the transplant over a two-year period.

2.5. Transplant monitoring

2.5.1. Coverage

To monitor the evolution of the Transplant meadow (seagrass coverage), photos were taken seasonally over a period of 24 months (2 years). The photos were taken at low tide using a GoPro Hero 7 camera, a 4 m height tripod and a square frame (1 × 1 m) used as a scale for image processing (Fig. 2C).

Image processing workflow for coverage assessment followed the methodology proposed by Costa et al. (2022). GIMP (Version 2.10.24) software was employed to adjust the perspective of the photos and increase the saturation and contrast of the seagrass leaves in relation to the sediments, while ImageJ (Version 1.52q) software was employed to calculate the coverage (%), based on a threshold colour selection.

2.5.2. Seagrass biomass and metal(loid)s quantification

To assess the evolution of *Z. noltei* aboveground and belowground biomass and respective contaminant burden, five cylindrical cores (8 cm deep, 15 cm diameter) were collected seasonally from each site (Donor and Transplant meadow). After collection, samples were taken to the laboratory, where (living) leaves, roots and rhizomes were meticulously separated, washed with distilled water, wiped with laboratory paper, and weighed to calculate the aboveground and belowground fresh biomass mass per square meter (g m^{-2}).

After weighing, samples were freeze-dried at −50 °C and 0.06 bar for at least 48 h in a Unicryo MC-4 L-60C. The dried tissues were then homogenized using an electric mill and stored until metal(loid) analysis. The quantification followed the same protocols and methodologies used for sediment characterization (Section 2.3), differing only in the reference material. For the plant samples, the CRM ERM-CD200 was used, as it closely matched the matrix under study. The recovery rates for these analyses ranged between 93 % and 108 % (n = 10).

2.5.3. Pigment analysis and PAM fluorometry

The evolution of the overall condition of seagrasses was monitored in the first year after transplantation through the quantification of photosynthetic pigments (chlorophylls *a*, *b*, and carotenoids) and the assessment of seagrass photosynthetic performance through Pulse Amplitude Modulation (PAM) fluorometry.

Photosynthetic pigments were determined seasonally in leaves of *Z. noltei* collected in both the Donor and Transplant meadows. Fresh leaves were homogenized in 90 % acetone (5 mL) using a mortar and pestle and centrifuged at 4000*g* for 10 min. The supernatant was spectrophotometrically read at 663 (A663), 646 (A646) and 470 (A470) nm, in a plate reader (Infinite 200Pro). The pigment content was expressed in μg g^{-1} of fresh weight (FW). To calculate chlorophylls *a* (*Chla*), *b* (*Chlb*), and carotenoids (*Cx* + *c*), the following equations described by Lichtenthaler (1987) were used:

- $Chla = 12.21 \times A663 - 2.81 \times A646$ μg mL^{-1}
- $Chlb = 20.13 \times A646 - 5.03 \times A663$ μg mL^{-1}
- $Cx + c = (1000 \times A470 - 3.27 \times Chla\text{-}104 \times Chlb)/198$ μg mL^{-1}

The evaluation of photosynthetic efficiency was performed by Junior PAM fluorometer (Heinz Walz GmbH) in both *Z. noltei* meadows (Donor and Transplant).

During each campaign, rapid light-response curves (RLCs) were generated by exposing a minimum of three samples per meadow to 12 increasing actinic light levels (25, 45, 65, 90, 125, 190, 285, 420, 625, 820, 1150, 1500 μmol photons m^{-2} s^{-1}) for 10 s, following the methodology employed by Fonte et al. (2023). The curves were adjusted according to the method outlined by Eilers and Peeters (1988), and the following parameters were determined: light absorption efficiency (α, μmol m^{-2} s^{-1}), minimum saturation irradiance (E_k, μmol m^{-2} s^{-1}), and maximum electron transport rate (ETR_{max}). Based on these data, the physiological status of seagrasses was evaluated.

2.6. Statistical analysis

All results were statistically tested using the permutation multivariate analysis of variance (PERMANOVA), considering a 2-way crossed design. For the seagrass coverage percentage, we considered the factors year of the transplantation (2 variables: first and second transplantation) and season (4 variables: spring, summer, autumn and winter). For all other parameters (e.g. seagrass biomass, metal(loid) quantification, pigment analyses and photosynthetic efficiency parameters), the factors were site (Donor meadow and Target/Transplant site) and season. Prior to the PERMANOVA, each factor was tested for its dispersion around the centroid using the PERMDISP analysis. All analyses were done with the PRIMER v6 software with PERMANOVA+ add-on (Anderson et al., 2008). Significant differences were assigned for a p-value ≤ 0.05.

3. Results

3.1. Site selection

The hydrodynamic model results revealed that, across all scenarios tested, there were only small variations in the parameters studied (Supplementary Table 1). The observation points defined in the Delft3D model showed that the maximum water column depth ranged from 0.87 m to 1.49 m, while the estuarine currents at these points ranged from 0.28 m s^{-1} to 0.88 m s^{-1}.

The predicted emersion times were the parameters that showed the greatest discrepancies, indicating that some locations could remain almost permanently submerged (with emersion times of <5 min), while other areas (such as L5_2 and L5_6 in Fig. 1C) may experience emersion times exceeding 12 h during certain times of the year, making them less suitable for this seagrass species.

3.2. Site characterization

The exploratory campaign showed that physicochemical parameters (Supplementary Table 2) revealed lower salinity values at the Transplant site, while temperature and pH values were higher, particularly in the puddles of water. Regarding sediment characteristics, the percentage of organic matter was slightly lower at the Transplant site, while the fine fraction (<63 μm) was similar at both sites (Table 1).

The concentrations of metal(loid)s in the sediments (mg kg^{-1}) were significantly different between the two sites, with the Transplant site being more contaminated due to its proximity to the pollution source in Laranjo Bay. At this site, the concentrations of As, Cd, Cu, and Hg were notably higher compared to those in the Donor meadow sediments (Table 1). Despite the significant differences observed in the Transplant site, only Hg exceeded the Probable Effect Level (PEL, 0.7 mg kg^{-1} dry

Table 1

Organic matter (%), fine fraction (%) and metal(loid) concentrations (mg kg^{-1}) in surface sediments from the Donor site and the Target/Transplant Site, both without vegetation. Values are presented as means ± standard deviation of 5 replicates. Different superscript letters indicate statistically significant differences between sites at the 95 % confidence level.

		Donor site	Target/Transplant site
Organic matter (%)		$9.6 \pm 0.5^{(a)}$	$5.3 \pm 0.7^{(b)}$
Fine fraction (%)		$19 \pm 2^{(a)}$	$18 \pm 3^{(a)}$
Metal(loid)s (mg kg^{-1})	[As]	$16 \pm 1^{(a)}$	$24 \pm 1^{(b)}$
	[Cd]	$0.37 \pm 0.03^{(a)}$	$0.43 \pm 0.02^{(b)}$
	[Cu]	$19 \pm 0^{(a)}$	$20 \pm 0^{(b)}$
	[Hg]	$0.71 \pm 0.08^{(a)}$	$1.8 \pm 0.5^{(b)}$
	[Ni]	$16 \pm 0^{(a)}$	$13 \pm 0^{(b)}$
	[Pb]	$25 \pm 2^{(a)}$	$21 \pm 0^{(b)}$
	[Sn]	$2.7 \pm 0.1^{(a)}$	$2.1 \pm 0.1^{(b)}$
	[Ti]	$1060 \pm 31^{(a)}$	$675 \pm 23^{(b)}$
	[U]	$2.9 \pm 0.1^{(a)}$	$2.7 \pm 0.2^{(a)}$
	[Zn]	$135 \pm 9^{(a)}$	$140 \pm 3^{(a)}$

weight) from the Canadian standards for marine sediment quality (CCME, 2002).

3.3. Transplant evolution, coverage and biomass

The evolution of the Transplant meadow over time (Fig. 2D to M) was analysed based on the vegetation coverage (Fig. 3A). The expansion of the *Z. noltei* meadow mainly coincided with the spring/summer months, maintaining its coverage constant in the autumn/winter months.

Data from the first transplant (July 2020) indicated that in the first year, the transplanted meadow expanded ≈60 % from the initial area, completely filling the spaces between patches after 15 months (Autumn 2021 — coverage of ≈95 %). There were only small deviations related to punctual erosion in the outermost areas most exposed to estuarine currents. After the first successful transplant, a second transplant (at the end of August 2021) was performed, extending the transplant area up to the natural *Z. noltei* patch. The expansion rates of this second transplant were similar to those observed in the first one, and after one year, the second transplant already had a coverage area of 84.3 ± 10.5 %. There were differences between seasons, particularly in the first year after the transplant (Fig. 3A, $p \leq 0.05$). However, when comparing the seagrass coverage values for the autumn, winter, spring, and summer seasons across the different transplants (e.g., comparing the first transplant in autumn 2020 with the second transplant in autumn 2021, both at 3 months post-transplant), no significant differences were observed between the two transplants.

Regarding plant biomass (below- and aboveground), a seasonal pattern was observed (Fig. 3B). In the Transplant meadow, the biomass remained stable for the first few months after transplantation (approximately 45 g m^{-2} for aboveground biomass and approximately 30 g m^{-2} for belowground biomass), followed by a significant increase between winter and spring in both plant sections, resulting in a doubling of biomass (from 44 to 86 g m^{-2} for aboveground biomass and from 30 to 74 g m^{-2} for belowground biomass). The maximum value for belowground biomass was reached in spring, while for aboveground biomass, it was in summer, with both subsequently decreasing until the following winter season. Similar results were also observed in the Donor meadow (Fig. 3B). Significant differences ($p \leq 0.05$) in plant biomass between Donor meadow and Transplant meadow were only evident during the initial post-transplant year (winter 2020 for both above- and belowground, and spring 2021 for aboveground biomass). Subsequently, both meadows exhibited comparable biomass values at each sampling period. Furthermore, analysing biomass over time for both meadows (Donor and Transplant) revealed significant differences ($p \leq 0.05$, Fig. 3B), indicating a seasonal pattern of biomass variation over time.

3.4. Hg accumulation by *Zostera noltei*

Based on the sediment characterization, the only potentially toxic element of concern in the Transplant site was Hg, justifying its quantification in both the aboveground and belowground biomass of *Z. noltei*. This was done seasonally over a two-year period for both the Transplant and Donor meadows (Fig. 3C).

Results revealed that Hg concentrations were consistently higher in the belowground biomass than in the aboveground biomass in both meadows. Indeed, significant differences ($p \leq 0.05$) were consistently observed in the Hg concentrations between the two meadows (Donor and Transplant), in both biomasses for the same season. In the Donor meadow, Hg concentrations remained relatively stable over time, ranging from 0.04 to 0.07 mg kg^{-1} in aboveground biomass and from 0.07 to 0.12 mg kg^{-1} in belowground biomass. Conversely, Hg concentrations in Transplant plant tissues exhibited greater variations, ranging from 0.13 to 0.19 mg kg^{-1} in aboveground biomass and from 0.20 to 0.46 mg kg^{-1} in belowground biomass. The highest Hg concentrations in both *Z. noltei* tissues were observed in spring/summer and the lowest in autumn for both meadows. Significant differences were observed over time in the aboveground biomass of the Donor meadow (Fig. 3C), while significant differences were only detected in the Transplant meadow during the spring season of 2022. Regarding Hg in belowground biomass, significant differences were only observed in the Donor meadow between summer 2020 and winter 2021, and in the Transplant meadow between autumn 2020 with winter 2020, summer 2021, winter 2021, and spring 2022.

The translocation factor (the ratio of Hg concentration between aboveground/belowground biomass) was always lower than 1 (Table 2), with the highest values observed in winter 2020 in the Donor meadow (translocation factor of 0.71) and in autumn 2020 in the Transplant meadow (translocation factor of 0.67).

3.5. Photosynthetic pigments and photosynthetic efficiency

The results for photosynthetic pigments (Table 3) revealed that chlorophyll *a* were consistently higher than chlorophyll *b* and carotenoids, with similar values for the latter two pigments over time. Seasonal variations in photosynthetic pigments were also observed, with only one significant difference ($p \leq 0.05$) between meadows in chlorophyll *a* during the spring of 2021.

Overall, photosynthetic efficiency parameters followed the same pattern in the two sites (Fig. 4). Light absorption efficiency (α) was significantly higher in winter in Donor and Transplant meadows (0.46 ± 0.06 and 0.28 ± 0.03 μmol m^{-2} s^{-1}, respectively, Fig. 4A). At the same time, significant differences were observed between these two meadows in this season. The lowest ETR_{max} (maximum electron transport rate) values (Fig. 4B) were recorded in spring 2021 for both meadows (56.9 ± 1.8 for Donor meadow and 75.8 ± 20.2 for Transplant meadow). Finally, the minimum saturating irradiance (E_k) values decreased in winter (Fig. 4C) for both meadows, with the lowest values recorded as 143.9 ± 16.3 μmol m^{-2} s^{-1} (Donor meadow) and 326.3 ± 82.3 μmol m^{-2} s^{-1} (Transplant meadow). In spring and summer season, the Transplant meadow plants presented significantly higher ETR_{max} and E_k values than the Donor meadow.

4. Discussion

4.1. Site selection

In the context of ecological restoration, where costs and uncertainties are inherent, meticulous prior planning is crucial to mitigate the risks of failure. A fundamental approach to risk minimization involves conducting a comprehensive evaluation of local environmental conditions. As an initial step for this active restoration program, the resilience of seagrasses to local sediment conditions was investigated in the laboratory by Fonte et al. (2023) and Oliveira et al. (2024), resulting favourable data and conclusions for their in-situ implementation. However, while the resistance of *Z. noltei* to contaminants present in the sediment of the study area is promising, it does not guarantee adaptation to the local environment and other abiotic conditions, particularly due to the complexity of local conditions (e.g., hydrodynamics). Thus, modelling emerged as an indispensable tool for assessment of the local hydrodynamic conditions, enabling the simulation of the spatial and temporal conditions and the projection of scenarios to evaluate the responses of hydrodynamic variables known to influence the seagrass establishment (Alekseenko et al., 2017; Azevedo et al., 2016; Erftemeijer et al., 2023; Valle et al., 2015; van Katwijk and Hermus, 2000), thereby providing crucial insights for the success of transplantation efforts.

For vegetation transplantation, a thorough understanding of parameters such as current velocity, maximum depth, and emersion time is indispensable, as each exerts a significant influence on the survival of seagrasses and habitat stability (Erftemeijer et al., 2023).

Analysing current velocities is relevant for mitigating the risk of erosion and uprooting of seagrasses, emphasizing the role of velocity in

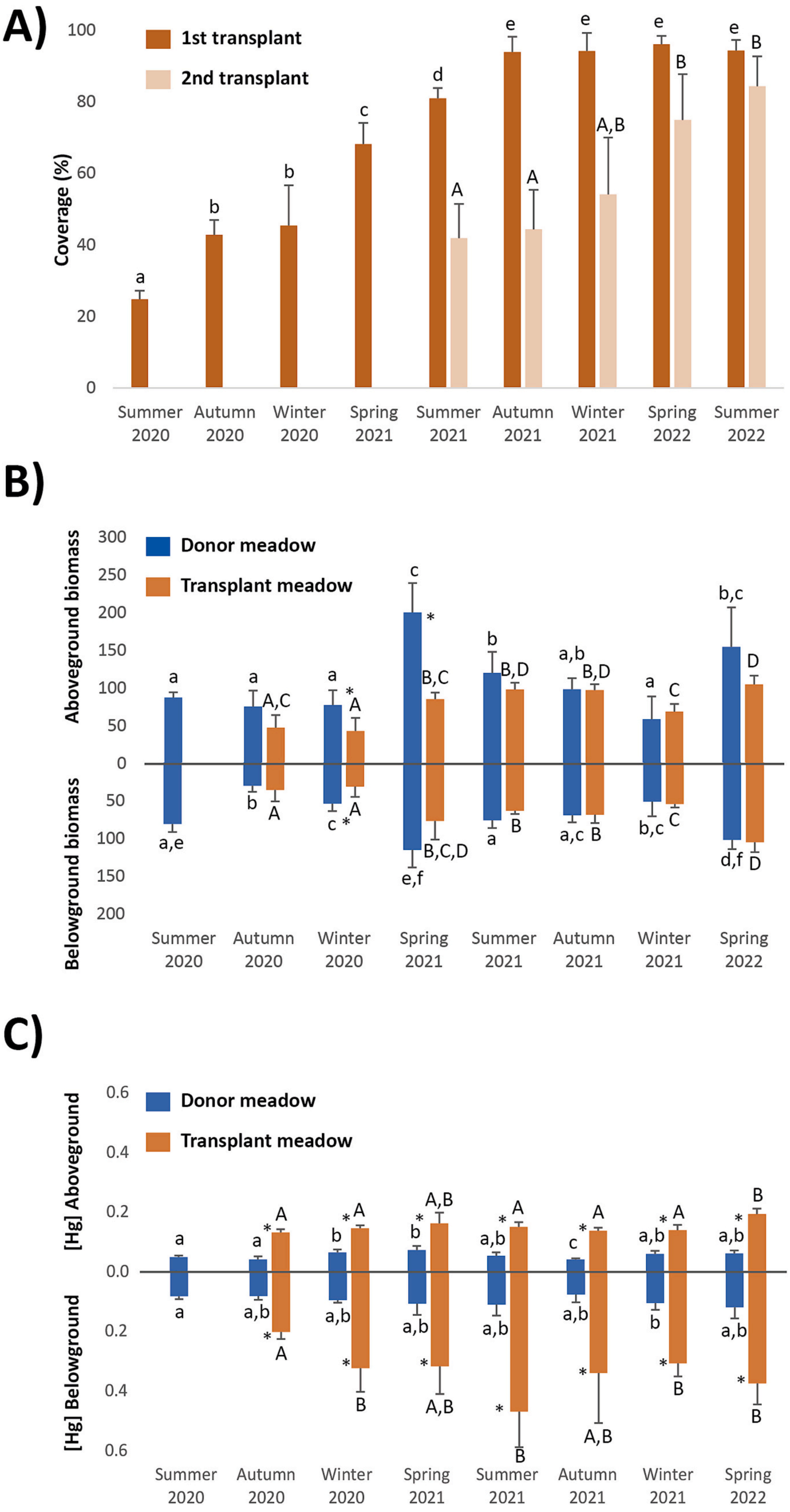

Fig. 3. Evolution of the seagrass coverage (%) (A) in the two transplants performed along the study period, evolution of the fresh aboveground biomass (g m^{-2}) and belowground biomass (g m^{-2}) (B) and Hg accumulation (mg kg^{-1}) in both tissues (C) over the 2 years. Different superscript letters indicate significant differences ($p \leq 0.05$) between the seasons. Asterisk (*) denotes significant differences between the Donor and Transplant meadow within the same season.

Table 2

Z. noltei translocation factor (Hg concentration ratio between aboveground/belowground) over time in the two meadows.

Meadow	Summer 2020	Autumn 2020	Winter 2020	Spring 2021	Summer 2021	Autumn 2021	Winter 2021	Spring 2022
Donor	0.63	0.52	0.71	0.71	0.51	0.56	0.59	0.54
Transplant	–	0.67	0.46	0.53	0.33	0.42	0.47	0.53

Table 3

Quantification of chlorophylls *a* and *b* and carotenoids (μg g^{-1}) over time. Different superscript letters indicate significant differences ($p \leq 0.05$) among seasons. Asterisk (*) denotes significant differences between the Donor and Transplant meadow within the same season.

		Donor meadow	Transplant meadow
Chlorophyll *a*	Summer 2020	$0.50 \pm 0.14^{(a)}$	
	Autumn 2020	$0.69 \pm 0.16^{(a,b)}$	$0.74 \pm 0.11^{(a)}$
	Winter 2020	$0.86 \pm 0.17^{(b)}$	$0.82 \pm 0.16^{(a,b)}$
	Spring 2021	$0.62 \pm 0.07^{(a)*}$	$0.76 \pm 0.07^{(a)*}$
	Summer 2021	$0.84 \pm 0.09^{(b)}$	$0.92 \pm 0.08^{(b)}$
Chlorophyll *b*	Summer 2020	$0.21 \pm 0.08^{(a,b)}$	
	Autumn 2020	$0.24 \pm 0.06^{(a,b)}$	$0.24 \pm 0.04^{(a)}$
	Winter 2020	$0.32 \pm 0.06^{(a,c)}$	$0.26 \pm 0.06^{(a)}$
	Spring 2021	$0.22 \pm 0.02^{(b)}$	$0.27 \pm 0.03^{(a)}$
	Summer 2021	$0.34 \pm 0.06^{(c)}$	$0.39 \pm 0.05^{(b)}$
Carotenoids	Summer 2020	$0.22 \pm 0.06^{(a)}$	
	Autumn 2020	$0.29 \pm 0.08^{(a,b)}$	$0.31 \pm 0.04^{(a,b)}$
	Winter 2020	$0.37 \pm 0.07^{(b)}$	$0.33 \pm 0.05^{(a)}$
	Spring 2021	$0.26 \pm 0.02^{(a)}$	$0.26 \pm 0.03^{(b)}$
	Summer 2021	$0.27 \pm 0.04^{(a)}$	$0.31 \pm 0.02^{(a)}$

preserving habitat integrity. The current velocity data in the various scenarios analysed indicated that the currents in the study areas were relatively low compared to findings by Koch (2001), who observed that some seagrass species, primarily subtidal species, could tolerate current speeds of up to 1.8 m s^{-1}. However, specific studies by Peralta et al. (2006) and Valle et al. (2014) with *Z. noltei* demonstrated that plants can acclimate to hydrodynamic stress, tolerating current speeds of 0.35 m s^{-1}. Thus, to ensure successful transplantation, areas with low hydrodynamics (current values between 0.20 and 0.60 m s^{-1}) were preferred.

Another key parameter is maximum depth, as at certain depths there may be insufficient light availability for plants, hindering photosynthesis, a fundamental process driving seagrass productivity and growth. Light unavailability can also be directly correlated with currents, as higher currents promote an increased amount of suspended particles in the water column (de Jonge et al., 2014; Dias et al., 2021; van Maren et al., 2015), which can diminish or block light penetration, thereby reducing photosynthetic performance when seagrasses are submerged. The depths obtained in various study locations (ranging from 0.87 m to 1.49 m) were relatively shallow compared to the water column depths in sea level rise vulnerability simulations for *Z. noltei* conducted by Ondiviela et al. (2020). These simulations assessed favourable, stressful, and unfavourable suitability conditions and found that even in environments with lower sand content (approximately 50 %), the plant adapted to depths of around 3 to 4 m. This suggests that at the shallow depths observed across different study locations, combined with the low currents, there is sufficient light penetration throughout the water column, allowing *Z. noltei* leaves to perform photosynthesis when submerged.

Furthermore, the duration of emersion periods plays a critical role in seagrass resilience. Although species like *Z. noltei* utilize brief periods of air exposure to assimilate CO_2 (Suykerbuyk et al., 2018), prolonged exposure to air and sunlight can result in desiccation, dehydration, cellular damage, and osmotic stress due to desiccation and high salinity. For instance, according to Leuschner et al. (1998), air exposure per tide may cause a 50 % water loss in leaves, accompanied by a 50 % reduction in photosynthetic rates, which in extreme cases may lead to decreases in mechanical strength and subsequently increase the probability of leaf sloughing (Suykerbuyk et al., 2018; Vermaat et al., 1993). Additionally, this can lead to shorter leaf lengths, as dehydrated leaf tips are prone to breakage, resulting in decreased photosynthetic capacity (Boese et al., 2003). On the other hand, prolonged exposure to high salinities can diminish photosynthetic performance due to ionic toxicity, alterations in the structure and functioning of the photosynthetic apparatus (e.g., PSI and PSII proteins and RuBisCo), and/or pigment degradation (Buapet, 2017). Conversely, intertidal plants submerged for extended periods, as mentioned earlier, may face a higher risk of erosion and uprooting, as well as insufficient light for photosynthesis, impacting their growth and development.

To mitigate these potential risks that could lead to transplant failure, the analysis of emersion time results revealed that certain areas were unsuitable for transplantation due to emersion times either ≤5 min or ≥12 h in specific scenarios. Furthermore, among the remaining sites, another selection was made to choose those that exhibited similar results even during extreme events, considering the anticipated exacerbation of these events due to global warming (Lorenzo and Alvarez, 2022; Lukasová et al., 2021; Wu et al., 2021; Yin et al., 2021), thereby ensuring the long-term success of the transplant. Sites with significant variation between scenarios were eliminated or considered unsuitable for transplantation.

Following a rigorous selection process, area 4 was identified as the most suitable for implementing the pilot transplant to restore the historically contaminated area. Among the potential locations in area 4, location L4_2 (marked by a red dot in Fig. 1C) was found to be the most suitable for transplantation. This location exhibited relatively low and consistent current velocities in all scenarios (approximately 0.34 m s^{-1}), a maximum emersion time of <10 h, and a maximum depth of approximately 1.20 m, found suitable for the survival of transplanted seagrasses. In addition, the modelling results were validated by mapping (2019) of a small *Z. noltei* meadow in Laranjo Bay, nearby location L4_2 (Sousa et al., unpublished data).

4.2. *Transplant and monitoring*

After considering the numerical modelling results and the sediment characterization, which revealed that only Hg concentrations exceeded the PEL reference value, but found to be tolerable by the plants (Fonte et al., 2023), an in-situ transplantation was carried out using *Z. noltei* patches. Although the choice of the best technique for transplant programs has been widely debated due to variable survival rates among different methods (Paulo et al., 2019; Proença et al., 2019; Suykerbuyk et al., 2016; Valle et al., 2015), the use of patches showed positive results in Laranjo Bay.

These positive results are evidenced by the analysis of coverage data, which revealed a progressive increase over time, with greater expansion of *Z. noltei* during the spring. Similarly, an increase was observed in aboveground and belowground biomass during spring, even in sites exposed to elevated As, Cd, Cu and Hg concentrations. Similar results of increased coverage and biomass during spring were observed by Sousa et al. (2019), Wong et al. (2020), Ruesink et al. (2022) and Sfriso et al. (2022) for different seagrass species. Furthermore, the similarity in biomass values between the Transplant meadow and the Donor meadow after 1 year of transplantation (summer 2021 onwards) indicates the effectiveness of the transplantation process and the complete adaptation of *Z. noltei* to the new location, with the Transplant meadow exhibiting similar profiles to the Donor meadow. From this point on, the observed variations mainly reflect seasonal changes.

The photosynthetic pigments and photosynthetic efficiency data between meadows, reflected the plant adaptation to the conditions on

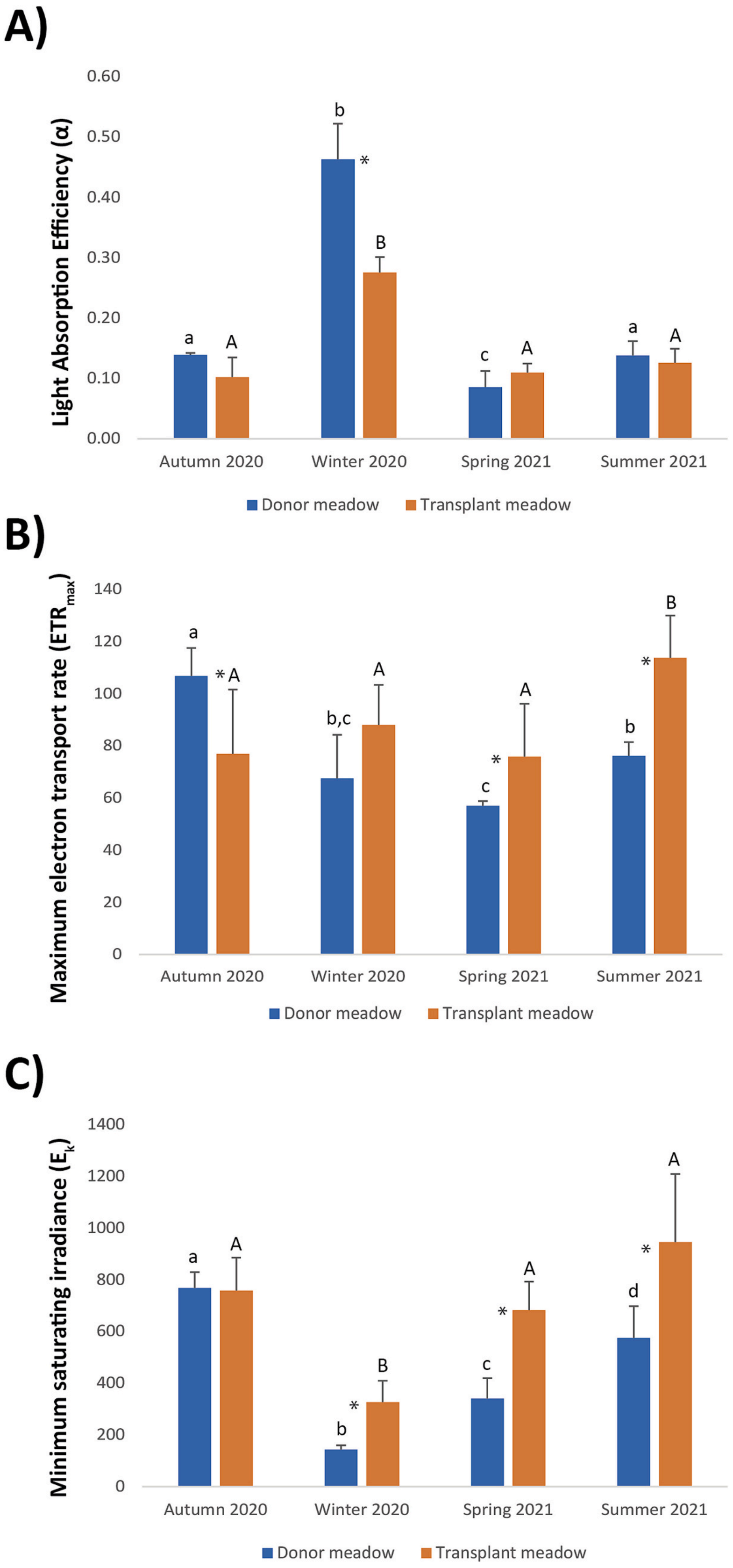

Fig. 4. Quantification of Light absorption efficiency (α — μmol m^{-2} s^{-1}) (A), Maximum electron transport rate (ETR$_{max}$) (B) and Minimum saturating irradiance (E$_k$ — μmol m^{-2} s^{-1}) (C). Different superscript letters indicate significant differences ($p \leq 0.05$) between the seasons. Asterisk (*) denotes significant differences between the Donor and Transplant meadow within the same season.

the Transplant site once again. In both meadows, *Z. noltei* was able to optimize light absorption and photosynthetic activity in response to the variable light conditions experienced throughout the different seasons, demonstrating that *Z. noltei* in both meadows were in good condition. A clear example of this adaptation was the winter of 2020, in which higher α values and lower ETR_{max} and E_k values were observed to compensate for the reduced light availability during this season, demonstrating that *Z. noltei* was able to photo acclimate in both meadows.

Higher pigment concentrations were detected in winter 2020 in both meadows and lower concentrations in summer 2020, following a general trend for angiosperms and marine plants, where pigment concentration increases with decreasing light availability to mitigate potential reductions in photosynthesis (Abal et al., 1994; Bargain et al., 2013; Mercado et al., 2003). This highlights once again the adaptability of *Z. noltei*. However, an abnormal pattern was observed in summer 2021, with pigment concentrations equal to or higher than those observed in winter 2020, presenting identical results to those observed by Bargain et al. (2013) for the same seagrass species. This increase in pigments during this season could be attributed to the fact that samples were collected towards the end of summer, when atmospheric conditions were already approaching autumn, resulting in an increase in pigment production to compensate for the reduction in light availability. Another explanation could be the high seagrass cover during this season, which may lead to leaf overlap and, indirectly, self-shading, resulting in a plant response by increasing pigment concentrations.

Given the data on *Z. noltei* coverage, biomass, photosynthetic pigments, and photosynthetic efficiency, it is evident that the contamination present in sediments of Laranjo Bay was not influencing the normal growth, expansion, physiological, and photosynthetic functions of this seagrass. Similar findings were reported by Fonte et al. (2023) and Oliveira et al. (2024) in a mesocosm experiment, where they studied the metabolic response and photosynthetic efficiency of *Z. noltei* when exposed to varying concentrations of metal(loid)s in sediments. To complement this information, an additional exploratory campaign was conducted in the summer of 2024 at the study site, revealing that numerous spontaneous patches began to appear around the Transplant site between 2022 and 2024 (locations of these patches are shown in Supplementary Fig. 1). This suggests natural recovery of the area through sexual reproduction (seed production and dispersal).

Even though the vital processes of seagrasses were apparently not influenced by contamination, a higher concentration of Hg was detected in the spring/summer seasons, as also observed by Fonte et al. (2023). This phenomenon is associated with plant growth and, in turn, with a higher metabolic rate of plants during this period, influenced by abiotic factors such as higher temperature and light availability. These conditions favour transpiration processes, which increases the plants' demand for water and nutrients. Indirectly, the roots also absorb more metal (loid)s (e.g., Hg), from the sediments, which are then translocated to the leaves (however, the translocation factor never exceeded 1 in both Donor and Transplant meadows), leading to lower Hg concentrations in the aboveground compared to the belowground tissues.

Apart from seasonal variation, a gradual accumulation of Hg was observed in transplanted plant tissues until reaching equilibrium (summer 2021) with the contaminants present in the sediment of Laranjo Bay. From this point on, a seasonal pattern became evident, with Hg concentrations in tissues primarily influenced by the effect of temperature on biogeochemical processes in sediments and plant activity. This gradual increase in Hg concentration, mainly observed in belowground biomass, may be attributed to the transplantation process, as *Z. noltei* patches were transplanted with approximately 5 cm of original and uncontaminated sediment, which may have protected the roots from surrounding metal(loid)s (e.g. Hg), as described by Fonte et al. (2023). Over time, diffusion processes would expose the roots to surrounding metal(loid)s, increasing Hg absorption until equilibrium was reached.

This accumulation pattern and adaptation to adverse conditions may result from the various mechanisms that plants possess. Specifically, when introduced into unvegetated areas, the plant gradually oxygenates anoxic sediment layers through photosynthesis and oxygen transport to belowground tissues, significantly impacting sediment biogeochemical cycles and stimulating the formation of iron and manganese oxides (Armstrong, 1967; Li et al., 2023). These compounds have a strong affinity for trace elements such as Hg, thus reducing their reactivity and availability to fauna and flora (Eckley et al., 2020; Godinho et al., 2014; Oliveira et al., 2023). Furthermore, within the oxidized layer, inorganic Hg can bind to organic matter, forming Hg-OM complexes, further reducing its availability (Dent et al., 2014; Duvil et al., 2018; Li et al., 2023; McCord et al., 2016). In addition, when these metal(loid)s are absorbed by the tissues, internal defence mechanisms can be activated, such as the synthesis of phytochelatins (Negrin et al., 2017; Nguyen et al., 2017; Turull et al., 2017) and metallothioneins (Samuel et al., 2021; Sruthi et al., 2017). Phytochelatins are low molecular weight peptides, whereas metallothioneins are proteins, both having high affinity for metal(loid)s and can bind to them, reducing their toxicity. Finally, as a last resort, when plants undergo oxidative damage due to metal(loid)s, seagrasses can activate antioxidant mechanisms, such as superoxide dismutase, catalase, and glutathione, to neutralize free radicals and protect the cells (Ferrat et al., 2002, 2003; Greco et al., 2019; Lin et al., 2016).

When compared with historical Hg bioaccumulation in the area, data from Coelho et al. (2009) for the same seagrass species reveal a gradual decrease in Hg concentrations in both biomass over the years. This trend may indicate an ongoing natural attenuation process, supported by the decline in contaminant content in surface sediment layers (Oliveira et al., 2018). The decline in Hg concentration highlights the vital role of the plant in facilitating the natural recovery of the coastal lagoon system by silting the most contaminated layers.

In summary, the adaptation of *Z. noltei* transplants in a historically contaminated area resulted from a combination of factors, from ongoing natural attenuation to local hydrodynamic conditions, plant resistance and successful transplant method. The use of seagrass patches with a 5 cm sediment layer (plant rhizosphere) helped mitigate plant stress when exposed to a distinct, more adverse biogeochemical environment (Suykerbuyk et al., 2016) and helped create favourable conditions for the plant to survive and gradually adapt to the new area, as also described by Costa et al. (2022). Additionally, the transplantation method minimizes damage to the roots and rhizomes (Costa et al., 2022; Valle et al., 2015) and helps in the self-facilitation processes (involving a series of adaptive mechanisms that plants develop to promote their own growth and survival), making it a promising technique for seagrass transplantation programs.

5. Conclusion

The pilot transplantation of *Zostera noltei* to a historically contaminated area was successful, demonstrating its potential as a Nature-based Solution for the ecological restoration of historically contaminated estuarine mudflats. The numerical modelling was a valuable tool in predicting the optimal area for transplant and simulating different scenarios. The transplanting method used (patch) enabled the gradual adaptation of seagrasses to the new environment, which was crucial for the successful rehabilitation and restoration of the target area.

Over two years, the Transplant meadow showed an increase in coverage area, forming a compact *Z. noltei* meadow of 50 m^2 reflecting the plant's adaptation to the local conditions and the plants resistance to metal(loid)s contamination.

While seasonal differences were observed in aboveground and belowground biomass, as well as in Hg concentration in plant tissues, the condition of the plants did not seem to be affected, as reflected by its photosynthetic efficiency.

Overall, this study serves as a valuable outcome for future restoration projects, particularly in light of the recently approved European Nature Restoration Law and United Nations Decade on Ecosystem Restoration, which prioritizes the restoration of degraded ecosystems.

CRediT authorship contribution statement

Vítor H. Oliveira: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **B.A. Fonte:** Investigation. **A. I. Sousa:** Writing – review & editing, Resources, Methodology, Investigation, Formal analysis. **D. Crespo:** Writing – review & editing, Investigation, Conceptualization. **J.M. Dias:** Writing – review & editing, Software, Resources. **N. Vaz:** Writing – review & editing, Software, Resources. **D. Matos:** Writing – review & editing, Investigation. **E. Figueira:** Writing – review & editing, Resources. **M.E. Pereira:** Writing – review & editing, Resources. **A.I. Lillebø:** Writing – review & editing, Resources. **M. Dolbeth:** Writing – review & editing, Investigation, Formal analysis, Conceptualization. **J.P. Coelho:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author(s) used ChatGPT in order to improve the language and readability of manuscript. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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.2024.178257.

Data availability

Data will be made available on request.

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