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The effect of Zostera noltei recolonization on N and P fluxes at the sediment/water interface

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ABSTRACT

Within the scope of an ongoing seagrass active restoration program at Ria de Aveiro, Portugal, the present work aimed at evaluating the recovery of *Zostera noltei* meadow nutrient regulation ecosystem function, by mediating Nitrogen and Phosphorus biogeochemical processes, and translated on the nutrient fluxes (PO_4-P, NO_x-N and NH_4-N) at the sediment/water interface. This plant-mediated process was evaluated seasonally at three sites (Bare bottom, *Zostera noltei* Transplant and Natural meadow) and at two tidal conditions which required two distinctive methodologies: (a) the low tide pools during ebb, and (b) flux chambers during high tide. Sediments were collected in situ and physicochemical parameters determined.

At *Zostera noltei* transplanted areas, plant-mediated biogeochemical processes were found to reduce nutrient fluxes (both NH_4-N and PO_4-P) at the sediment/water interface, and its significance varied seasonally and along the tidal cycle. Furthermore, nutrient fluxes for both vegetated sites (Transplant and Natural) were similar, showcasing that the N and P biogeochemical processes and function were re-established no later than a year after transplantation.

1. Introduction

Estuarine ecosystems are characterized by being transition environments between rivers' freshwater and oceans' salt water, being therefore highly dynamic environments. Its interface with the terrestrial areas, from which they receive matter and energy, promotes productivity, and contributes to increased biodiversity and species richness within these ecosystems (Duffy, 2006).

Seagrasses are vital components of estuarine ecosystems and considered foundational species. These underwater flowering plants have various functions that contribute meaningfully to the improvement of water quality and overall ecosystem health (Bos et al., 2007). Historically, European seagrass meadows have faced significant challenges, such as poor water quality, coastal development, and climate change, leading to widespread habitat loss, particularly of the endemic species *Posidonia oceanica* in the Mediterranean (de los Santos et al., 2019). However, recent studies suggest a more nuanced situation, where reversal and stabilization of declining trends are becoming evident, contrasting with global patterns of continued decline (Costa et al., 2022; Danovaro, 2020; Dunic et al., 2021). Current literature emphasizes that many areas are witnessing a resurgence in seagrass coverage, underscoring the possibility of a more optimistic outlook for certain meadows. In locations like Portugal, Spain, and France, increases in biomass have been documented, indicating that specific environments are regaining ecological balance (Danovaro, 2020; Sousa et al., 2019).

One of the primary functions of seagrasses is their ability to improve water quality through various mechanisms, including nutrient filtration, sediment stabilization, and wave attenuation (Duarte et al., 2013). Seagrasses can trap sediments and organic matter, thereby preventing resuspension and reducing turbidity in coastal waters (Bos et al., 2007; Bulmer et al., 2018). This physical trapping often results in increased water clarity and improved light penetration, which is crucial for the growth of these plants themselves as well as for photosynthetic organisms in the ecosystem (Hendriks et al., 2008; Tang and Hadibarata, 2022). Furthermore, seagrass meadows enhance water quality by absorbing excess nutrients from the water column, particularly nitrogen and phosphorus (Bulmer et al., 2018). This nutrient uptake is critical in mitigating eutrophication, a process that leads to algal blooms and subsequent declines in oxygen levels in aquatic environments (de los Santos et al., 2019; Nordlund et al., 2024). The absorption of these nutrients helps restore balance to coastal ecosystems that have been disrupted by excess nutrient inputs, largely from agricultural runoff and

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urban sources (Greiner et al., 2013; Kusnadi et al., 2024).

The complex root and rhizome system presented by seagrasses facilitates the interactions between the sediment and the adjacent water column. The absorption of nutrients by seagrasses can reduce the fluxes of remineralized nutrients in the sediment/water interface, especially in periods of high plant activity (McGlathery et al., 2004). The source-sink function of seagrasses varies seasonally depending on their growth requirements: it can act as nitrogen sinks during their maximum growth and productivity season (spring-summer); and turn to a source of nutrients during its decay phase (autumn), when decomposition rates are high and plant nitrogen requirements are lower, according to McGlathery et al. (2004).

Seagrass restoration has been gaining momentum in recent years and will play a pivotal role in achieving the objectives set by the United Nations Decade on Ecosystem Restoration (2021–2030) (Resolution A/RES/73/284, (UN General Assembly, 2019)) and the EU Nature Restoration Law (Regulation (EU) 2024/1991, (EU, 2024)). These initiatives emphasize the urgent need for effective restoration practices aimed at reversing environmental degradation and enhancing the resilience of ecosystems, particularly in light of climate change and biodiversity loss (Regulation (EU) 2024/1991, Resolution A/RES/73/284, (EU, 2024; UN General Assembly, 2019)). In the Ria de Aveiro, the success of a *Z. noltei* restoration project (Oliveira et al., 2025) has been demonstrated through the recovery of ecosystem functions such as bioremediation (via phytostabilization, (Oliveira et al., 2023)) and improvement of local benthic biodiversity following transplantation (Crespo et al., 2023). However, there is no information on whether seagrass recolonization measures restore the nutrient regulation ecosystem function, and how long this recovery may take. While the positive effect of mature seagrass meadows on nutrient regulation is acknowledged, no information is available on the effect of restoration actions on this ecosystem function provided by seagrasses.

This research therefore aims to clarify and evaluate the recovery of seagrass associated nutrient dynamics ecosystem function, as a measure of restoration success. The specific objective of the present work was to evaluate the effect of a restored *Z. noltei* meadow on the seasonal nutrient fluxes (NH$_4$-N, NO$_x$-N, PO$_4$-P) at the sediment/water interface, compared to a natural meadow and non-vegetated sediment.

2. Materials and methods

2.1. Study site

Ria de Aveiro (Fig. 1A), a LTsER – Long-Term Socio-Ecological System platform –, is a shallow lagoon located on the Portuguese western coast (40°38′N, 8°44′W). This system is classified as a Special Protection Area and a Site of Community Importance under Natura 2000 network (Genua-Olmedo et al., 2023). It presents an extremely complex geometry, with great fluvial and tidal influence. Exchanges between the ocean and the interior of the lagoon take place throughout a single artificial

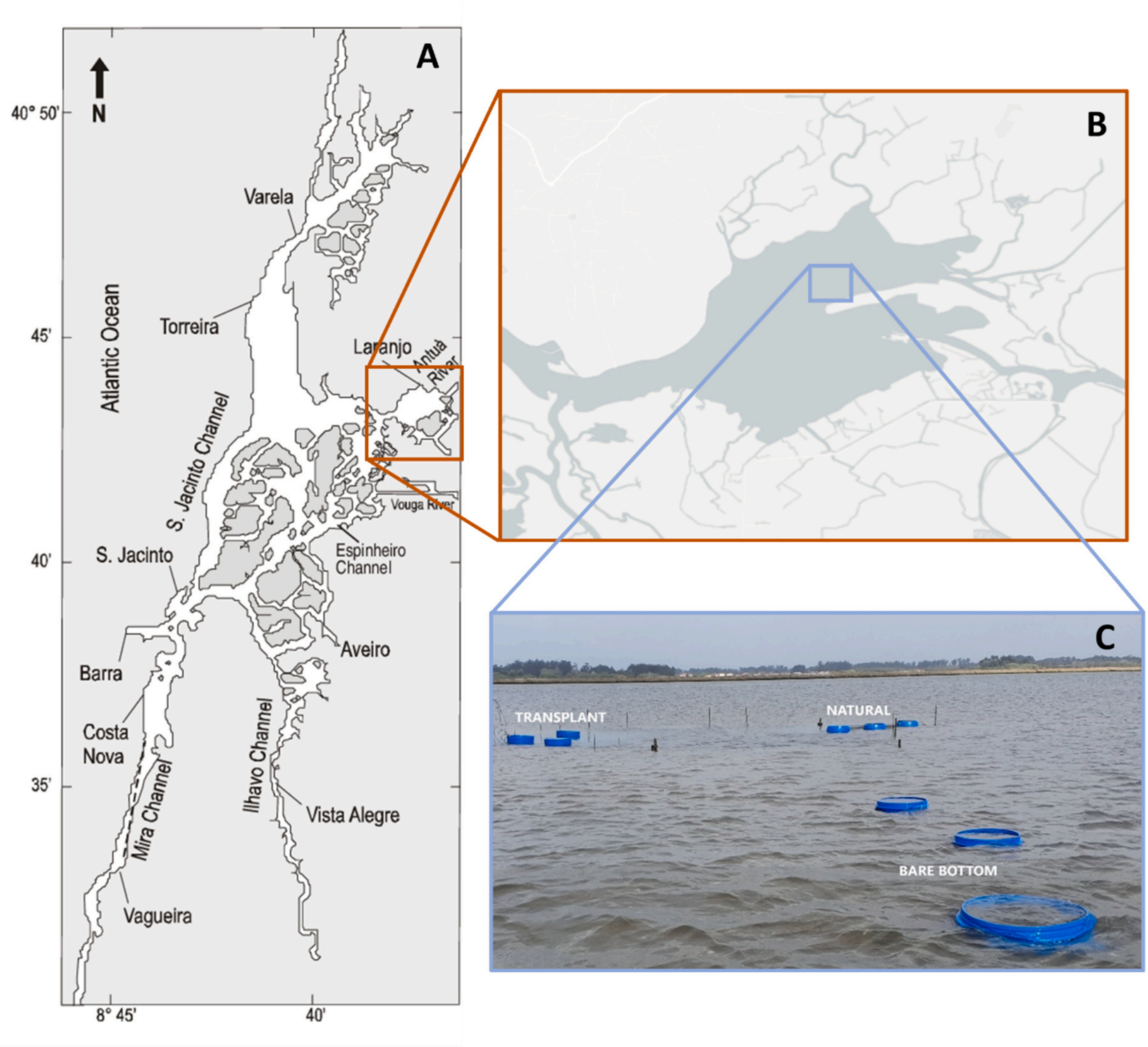

Fig. 1. Study site location. (A) Ria de Aveiro, (B) Laranjo Bay, (C) Sampling sites.

channel, 1.3 km long, 350 m wide and 20 m deep (Dias et al., 2000). Ria de Aveiro has been designated a mesotidal lagoon since the average tidal height variation is 2 m (minimum of 0.6 m during neap tides and a maximum of 3.2 m during spring tides). The tidal regime of this system is predominantly semidiurnal, having two high and low tides every 24 h. The wetland area is approximately 83 km^2 and 66 km^2 at high and low tide. Laranjo Bay (Fig. 1B) is a shallow basin (area of 2 km^2) inner to Ria de Aveiro, known to be historically contaminated (Oliveira et al., 2018). Although the discharge of effluents no longer occurs and a natural attenuation process is ongoing in the area, the contamination is still present in sub-surface layers of sediment at this bay, which may become biologically available in case of erosion events (Oliveira et al., 2018). Ecological restoration measures are currently underway at Laranjo Bay to address the historical contamination issue, namely the recolonization of intertidal plains with seagrass *Z. noltei* for sediment stabilization, which had significant impacts on the biogeochemistry of contaminants (Oliveira et al., 2023). The process of recolonization was carried out through *Z. noltei* sod transplants near (about 2–3 m) a small native meadow (area 5 m^2) found in 2019 at Laranjo Bay. The first transplant occurred in late July 2020 (area of 25 m^2) and at the end of August 2021 an expansion from 25 to 50 m^2 took place with a second transplant (Oliveira et al., 2025). Oliveira et al. (2025) verified seasonal changes in biomass, photosynthetic parameters, and also an increase in coverage area in the transplanted site. Specifically, in summer 2021, the coverage area for the 1st transplant was about 80 % and the aboveground biomass for this meadow was almost equal to the biomass of its donor meadow (Oliveira et al., 2025).

2.2. Field work

Four field campaigns were carried out between September 2021 and May 2022, representing the four late seasons of the year. Three specific sites (Fig. 1.C) were chosen for this study: a well-preserved *Zostera noltei* meadow (Natural), a *Z. noltei* meadow that had been recently recolonized (approximately 1 year before, Transplant), and adjacent sediment without vegetation (Bare bottom), distanced approximately 15 m from the vegetated sites.

To investigate nutrients in the intertidal pools, three PVC rings (Ø = 45 cm, h = 15 cm) were carefully positioned on the sediment at each site, following the methodology employed by Lillebø et al. (2010), on the day before each field campaign. Sampling began the following day, on an hourly basis (from t0 to t5), as soon as the top of the PVC rings emerged during ebb, lasting throughout the daytime until the flood. At each sampling instance and site, a 100 mL water sample was extracted using a syringe, stored in containers for subsequent processing and laboratory analysis. Simultaneously, physicochemical parameters (water temperature, salinity, pH, and dissolved oxygen) were measured using field probes (WTW pH/Cond 3320, Oxi 3310).

To assess nutrient fluxes during high tide, the methodology described by Lillebø et al. (2010) was implemented. Triplicate Plexiglas flux chambers (Ø = 12 cm, h = 52 cm) were positioned at each sampling site before the flood, filled with water from the main channel, and sealed with a flexible impermeable membrane during the flood. Water samples and physicochemical parameters were collected and measured under initial (main channel water) and final (flux chamber water and channel water) conditions of the flux experiment.

To evaluate sediment characteristics at each site, 10 cm sediment cores (Ø 3.5 cm) were collected and sectioned at two-centimeter intervals. These sediments were stored in respective bags for subsequent laboratory analysis.

2.3. Laboratory work

Following the field sampling, laboratory processing occurred on the same day. Water samples were filtered (pre-weighed and combusted GF/C filters, Ø 47 mm) and analyzed for suspended particulate matter (SPM, expressed in mg L^{-1}), organic matter content (OM, expressed in %), concentrations of dissolved inorganic nutrients (NH_4-N, NO_x-N, PO_4-P, expressed in μmol L^{-1}), and total dissolved organic carbon (TOC, expressed in ppm). For more information on physico-chemical parameters, SPM, OM and TOC data at intertidal pools and flux chambers, see Supplementary material, Tables S1 and S2.

The determination of dissolved inorganic nutrients' concentrations was performed using a segmented flow analyzer (SKALAR San + equipment), based on colorimetric methods, as used by Jerónimo et al. (2021). The total dissolved organic carbon was assessed using the Sievers InnovOx & InnovOx ES equipment (Sievers Instruments, 2018).

Nutrient fluxes (expressed in g m^{-2} h^{-1}) were calculated both during high and low tide periods at the flux chambers and intertidal pools, respectively. $Flux = (C_{t5} - C_{t0}) \times V_{H2O}/Area/time$, being C the concentration of each element (expressed in g m^{-3}) at the final (t_5) and initial (t_0) moments, V_{H2O} the volume of water (expressed in m^3) and time the 6 h passed between the initial and final sample.

To characterize the sediment at each site, salinity and pH values, organic matter content, and the fine fraction (particles <63 μm) of the top 10 cm of sediment were examined.

Salinity and pH in the sediments were determined by incubation in distilled water in a 1:5 ratio (msediment:Vwater), a 2 h stirring period (bioSan, Environmental Shaker – Incubator ES-20/60) followed by a 2 h resting period. The parameters were then measured with the respective probes.

The quantification of organic matter content utilized the loss on ignition method as described by Williams (1985). This process involved the incineration of a portion of the collected sediment samples at a temperature of 450 °C in a muffle furnace for a period of 5 h.

The fine fraction content (<63 μm) was determined using a sieve tower. Each sample was weighed and introduced into a vertical sieve shaker (Retsch A8200 basic) equipped with sieves of various openings: 1 mm, 500 μm, 250 μm, 125 μm, and 63 μm. Specifically, only the fine fraction, representing a blend of silt and clay particles according to the Wentworth (1922) scale, was considered for analysis. The resulting sediment fraction <63 μm was weighed, and the distribution of grain sizes was calculated relative to the total sample weight.

2.4. Statistical analysis

All data were analyzed using statistic software GraphPad Prism, version 8.0.2. Depending on parameter, and after testing for normality and homogeneity on raw data. The significant differences were tested using either Two-way ANOVA or RM Two-way ANOVA, this last with the Geisser-Greenhouse correction were used. Ordinary Two-way ANOVA was used when comparing data from intertidal pools and flux chambers for the same site (nutrient fluxes). Repeated Measures Two-way ANOVA was used when testing data sampled hourly throughout the tidal cycle (nutrient concentrations) within the same tidal pools. The factors Site (Transplant, Natural and Bare bottom) and Season (Summer, Autumn, Winter, Spring) were considered for intertidal pools and nutrient fluxes. Significant differences were considered for p-value ≤ 0.05. Results are presented as mean ± standard error of the mean.

The data obtained per unit of time from intertidal pools was modelled by nonlinear regression analysis, using GraphPad Prism version 8.0.2. The Second order polynomial (quadratic) model was used to fit data from water column nutrient concentrations. To assess the goodness of the fit of the experimental data, the coefficient of determination (R2) and the standard deviation of residues (Sx/y) were determined. A relatively high R2 and low value of Sx/y were used as criteria for good fit. For each case, the fitting was tested using three replicate concentrations at each studied time.

Principal Component Analysis was performed using PRIMER v.6, with normalized variables. PCA analysis was performed to reduce the dimensionality of data, which can help to identify patterns and relationships between the study sites and the variables analyzed.

3. Results

3.1. Sediment

Overall, no significant differences were observed for salinity, pH, organic matter content and fine fraction (Table 1) with increasing depth or between sites (2-way ANOVA, $P > 0.05$). Salinity values ranged between a minimum of 1.6 psu in autumn and a maximum of 3.1 psu during winter. In the case of pH, the lowest value was registered in spring, 6.7, and the highest value in winter, 7.2. Organic matter content varied between 4.5 % in winter and 6.1 % in summer. The fine fraction of the sediment presented the lowest values in autumn (19 %) and the highest values both in winter (Transplant, 27 %) and in summer (Bare Bottom, 27 %).

3.2. Water column

3.2.1. Dissolved inorganic nutrients

In summer (Fig. 2A), NH_4-N and NO_x-N concentrations (μmol L^{-1}) in intertidal pools were the highest at all sites, compared to other seasons. NH_4-N concentrations were similar between the two vegetated sites, and lower than the concentrations at the adjacent unvegetated site, which had an increase over the tidal cycle (from <1000 to about 2000 μmol L^{-1}). Therefore, statistically significant differences were found between sites (2-way RM ANOVA, $P = 0.0003$), in this season. NO_x-N concentrations reached values of approximately 1500 μmol L^{-1} and presented high variability, thus no significant differences were found between sites or along the tidal cycle (2-way RM ANOVA, $P > 0.05$).

In autumn (Fig. 2B), NH_4-N concentrations presented a similar pattern at vegetated sites, ranging within a restricted interval (between 40 and 80 μmol L^{-1}). In turn, NO_x-N concentrations presented an identic pattern and ranged between 60 and 100 μmol L^{-1} at all sites. Thus, no significant differences were found between sites or along the tidal cycle ($P > 0.05$), for both nitrogen compounds.

In winter (Fig. 2C), the lowest NH_4-N concentrations were recorded (<20 μmol L^{-1}), with similar values at vegetated sites and slightly higher values at the adjacent unvegetated site. Statistically significant differences were found between sites (2-way RM ANOVA, $P < 0.0005$) and along the tidal cycle (2-way RM ANOVA, $P = 0.0079$). In turn, NO_x-N concentrations presented a similar pattern at all sites, with high variability, ranging between 60 and 130 μmol L^{-1}. Statistically, NO_x-N concentrations were significantly different along the tidal cycle (2-way RM ANOVA, $P = 0.0059$).

Table 1
Salinity and pH values, organic matter content and fine fraction of the top 10-cm of the sediment. All data is presented as mean ± standard error, $n = 15$.

Season	Site	Salinity (psu)	pH	OM (%)	< 63 μm (%)
Summer	Transplant	2.4 ± 0.6	6.9 ± 0.1	5.1 ± 1.1	22 ± 5
	Natural	2.4 ± 0.4	6.8 ± 0.2	5.6 ± 0.8	21 ± 4
	Bare bottom	2.5 ± 0.4	6.9 ± 0.1	6.1 ± 0.8	27 ± 3
Autumn	Transplant	1.6 ± 0.3	7.2 ± 0.0	4.9 ± 1.3	19 ± 6
	Natural	1.9 ± 0.3	6.9 ± 0.1	5.6 ± 0.9	19 ± 4
	Bare bottom	1.6 ± 0.1	7.0 ± 0.1	5.0 ± 0.5	21 ± 2
Winter	Transplant	3.1 ± 0.6	7.3 ± 0.1	5.2 ± 0.9	27 ± 6
	Natural	3.1 ± 0.3	7.2 ± 0.0	5.9 ± 1.2	26 ± 3
	Bare bottom	2.9 ± 0.3	7.2 ± 0.1	4.5 ± 0.7	22 ± 4
Spring	Transplant	2.5 ± 0.4	6.9 ± 0.1	5.5 ± 1.0	23 ± 5
	Natural	3.0 ± 0.6	6.7 ± 0.1	6.0 ± 0.8	26 ± 5
	Bare bottom	2.7 ± 0.4	6.9 ± 0.1	5.8 ± 0.6	26 ± 2

In spring (Fig. 2D), both NH_4-N and NO_x-N concentrations were approximately constant and similar at all sites, with low concentrations, not exceeding 50 μmol L^{-1}. Statistically, significant differences were found for NH_4-N concentrations both between sites (2-way RM ANOVA, $P = 0.0053$) and along the tidal cycle (2-way RM ANOVA, $P = 0.0114$). In turn, no significant differences were observed for NO_x-N concentrations (2-way RM ANOVA, $P > 0.05$).

PO_4-P concentrations in intertidal pools (Fig. 3) were highest in the summer, ranging from 10 to 15 μmol L^{-1} and approximately similar in the vegetated sites (natural and transplanted meadows), while lower than the concentration in the adjacent unvegetated site (<20 μmol L^{-1}). During the tidal cycle, this concentration increased significantly in the adjacent site without vegetation (2-way RM ANOVA, $P = 0.0019$). In autumn, PO_4-P concentration was similar at vegetated sites (<1 μmol L^{-1}) and significantly higher at the adjacent area without vegetation. Statistically significant differences were observed, in this case, both between sites (2-way RM ANOVA, $P = 0.0005$) and along the tidal cycle (2-way RM ANOVA, $P < 0.0001$). In winter, PO_4-P concentration remained constant and similar in the three sites (2-way RM ANOVA, $P > 0.05$). Regarding spring period, the vegetated sites presented similar concentrations (<1 μmol L^{-1}), being lower than the concentrations in the adjacent unvegetated site, which had an increase from <1 to 2 μmol L^{-1}. In this period, statistically significant differences were found both between sites (2-way RM ANOVA, $P = 0.0340$) and along the tidal cycle (2-way RM ANOVA, $P = 0.0200$).

Overall, nutrient fluxes during low tide (Fig. 4) were always higher in summer season, and higher than high tide nutrient fluxes. NH_4-N flux was negative in vegetated sites (<10 g m^{-2} h^{-1}) and positive and with higher values in the adjacent unvegetated site (<30 g m^{-2} h^{-1}), in summer. Statistically significant differences were found both between seasons (2-way ANOVA, $P = 0.0067$) and sites (2-way ANOVA, $P = 0.0002$).

NO_x-N flux was negative in the natural meadow (<15 g m^{-2} h^{-1}) and adjacent sediment without vegetation (<20 g m^{-2} h^{-1}), being positive at the transplanted site (<10 g m^{-2} h^{-1}), despite no significant differences found between seasons or sites ($P > 0.05$).

PO_4-P flux was positive at all sites, presenting higher values in the adjacent unvegetated site (approximately 0.3 g m^{-2} h^{-1}), compared to the vegetated sites (<0.1 g m^{-2} h^{-1}). Significant differences were observed between seasons (2-way ANOVA, $P = 0.0005$), in this case.

Nutrient fluxes (g m^{-2} h^{-1}) during the high tide (Fig. 4), were significantly higher in summer, compared to other seasons. NH_4-N fluxes were negative in the natural (0.4 g m^{-2} h^{-1}) and transplant (0.2 g m^{-2} h^{-1}) sites. In turn, positive fluxes were recorded in the adjacent site without vegetation (<0.1 g m^{-2} h^{-1}), in the same period. Statistically, significant differences were found both between sites (2-way ANOVA, $P = 0.0203$) and seasons (2-way ANOVA, $P = 0.0078$).

NO_x-N fluxes were positive at all sites, being higher in the natural meadow (about 1.5 g m^{-2} h^{-1}) and lower in the adjacent sediment without vegetation (about 0.5 g m^{-2} h^{-1}), in summer season. Therefore, significant differences were found both between sites (2-way ANOVA, $P = 0.0043$) and seasons (2-way ANOVA, $P < 0.0001$).

PO_4-P fluxes were positive and similar at vegetated and unvegetated sites (about 0.01 g m^{-2} h^{-1}), in the same period. In this case, significant differences were found between seasons (2-way ANOVA, $P < 0.0001$).

3.2.2. Principal Component Analysis (PCA)

The first two components of this analysis justified 66.8 % of the total variation in summer, 68.2 % in autumn, 59.1 % in winter, and 60.8 % in spring.

In spring-summer period (Fig. 5A and B), the initial times of all sites were close and with the tidal evolution, while the vegetated sites

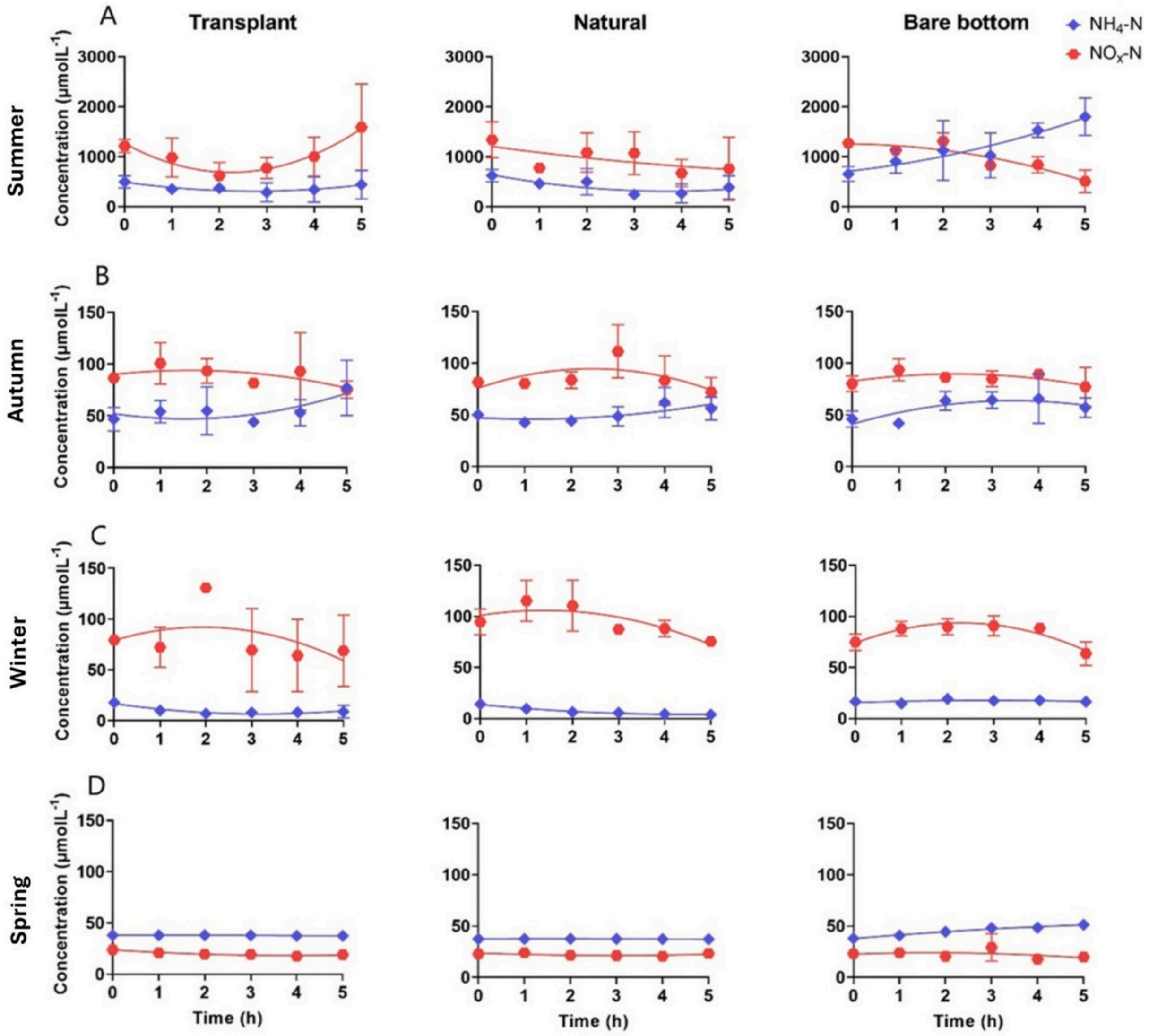

Fig. 2. NH_4-N and NO_x-N concentrations (μmol L^{-1}) in intertidal pools, (A) in summer, (B) in autumn, (C) in winter and (D) in spring season. All data is presented as mean ± standard error, $n = 18$. Fitted regression lines were added to plots to clarify the variation patterns.

remained clustered, the adjacent unvegetated site diverged. In addition, the distribution of vegetated site data was mainly related to pH and DO variables, while the adjacent unvegetated site was mainly associated with the nutrient concentrations (PO_4-P and NH_4-N).

In autumn (Fig. 5C) and winter (Fig. 5D), no clear separation was observed between sites nor along the tidal evolution, except for the adjacent Bare bottom site in winter, which was clustered.

4. Discussion

The in-situ measurements at Ria de Aveiro showcase the importance of recovering seagrass meadows, specifically *Z. noltei*, for the mediation of the N and P biogeochemical processes and nutrient dynamics (function) in the sediment and overlying water column.

Seagrasses are generally known as ecosystem engineers (Bos et al., 2007), as they reduce water flow velocities in their canopies. This usually leads to increased net sedimentation rates and reduction of the grain size distribution of sediments. Plant cover is also normally associated with higher sediment OM content (Lillebø et al., 2006). In the present research, sediment characteristics were found to be similar between vegetated and unvegetated sites, which could suggest a negligent effect of plant cover on sediment characteristics. However, a possible coexistence of multiple ecological and hydrological factors could mask the plants' effect on sediment characteristics. Similar findings were reported previously by McGlathery et al. (2012) and Orth et al. (2020) in newly colonized meadows (1 to 2 years), who found that significant differences between vegetated and unvegetated sites were only reported in natural meadows 7 to 9 years after their establishment. While it is known that the meadow coverage recovery may take <5 years, Borja et al. (2010) reports that the full recovery, in terms of process and function, of most coastal and estuarine ecosystems is only achieved after 25 years. These findings, while predictable for the transplant site, also suggest the studied natural meadow to result from a recent colonization event (but at least 3 years before the transplant), following the improvement of local environmental conditions. More importantly, the observed sedimentary phase similarity between sites highlights the fact that any variations observed in the water column nutrient content between sites (intertidal pools and flux chambers) were mostly forced by the effect of plant coverage, and not distinct sediment characteristics.

Overall, nutrient concentrations in intertidal pools in all study sites demonstrated a significant seasonal effect. Such seasonal differences will result from variations of rainfall, water temperature and salinity, as observed in both the intertidal pools and flux chambers (Tables S.1 and S.2). These variables, but also point source anthropogenic inputs and

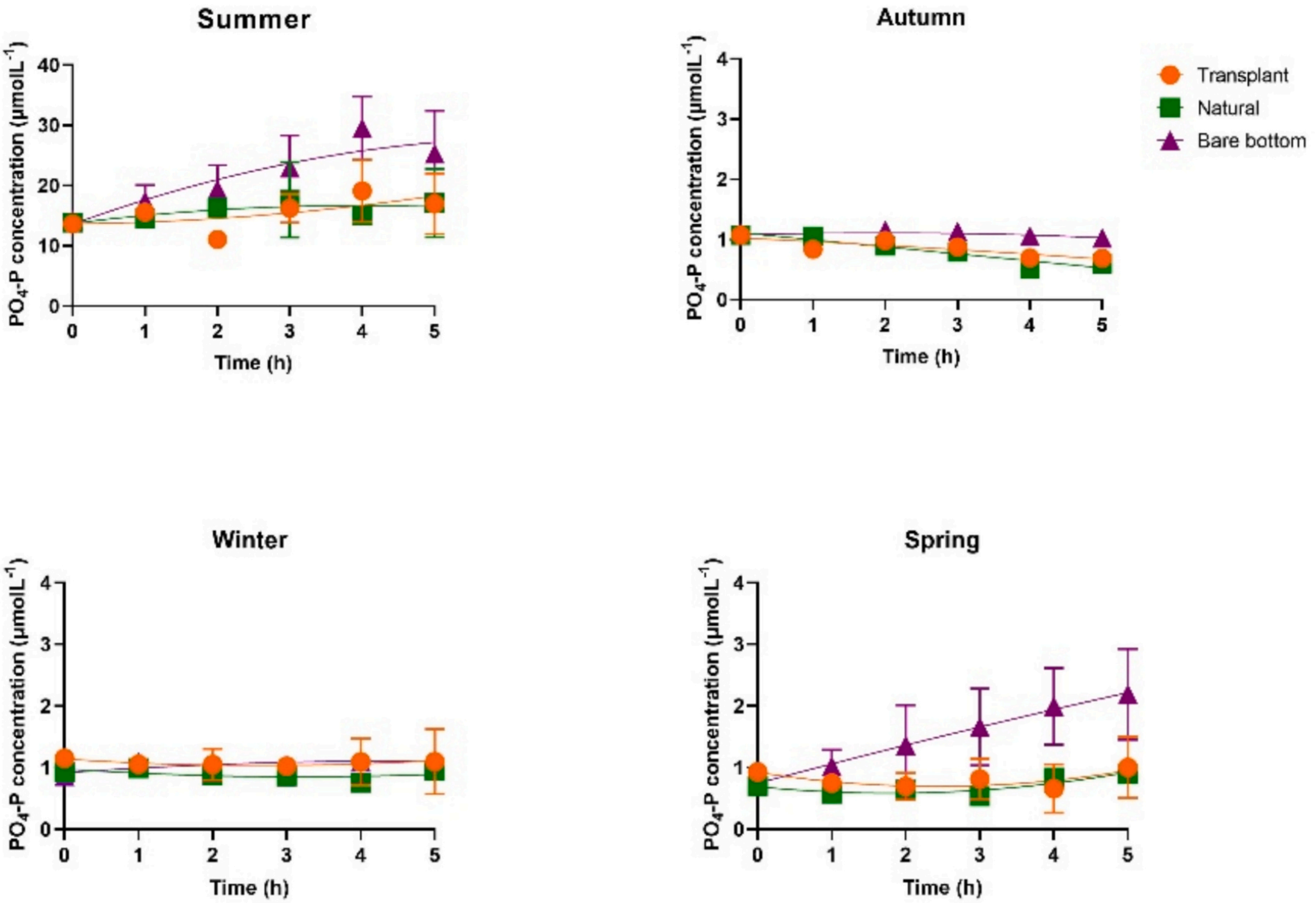

Fig. 3. PO_4-P concentrations (μmol L^{-1}) in intertidal pools, in each season. All data is presented as mean ± standard error, n = 18. Fitted regression lines were added to plots to clarify the variation patterns.

drainage, may influence both the input of nutrients from upstream areas but also increase or decrease the biogeochemical processes at the sediment/water interface. Differences observed between sites at each seasonal sampling moment, however, will result mainly from the effect of seagrass presence and its associated microbiome, which will mediate biogeochemical processes both in the sediment and the overlying water.

This is corroborated by the fact that significant differences between vegetated and non-vegetated sites occurred mostly in spring/summer, when plant activity is more significant.

NH_4 concentrations showed a decreasing trend in sites with *Zostera noltei*, contrary to unvegetated sites. In its period of greatest activity (spring/summer) (McGlathery et al., 2004), seagrasses can enhance nitrogen sequestration for its growth promoting the oxidation of the rhizosphere (Lillebø et al., 2006). As reported in Lillebø et al. (2002), the obtained results demonstrate a clear vegetation coverage influence (Reynolds et al., 2016), especially in the period of higher temperatures. The assimilation of nitrogen compounds by plants, bacteria and/or algae may justify the decrease in global ammonium concentrations in the water column of the vegetated sites (Bulmer et al., 2018). Some authors (Bulmer et al., 2018; Qu et al., 2007) recorded higher fluxes in winter at unvegetated sites. Bulmer et al. (2018) reported that with increased seagrass biomass, fluxes at the sediment/water interface were lower and inferior NH_4 concentration at vegetated sites compared to sites without vegetation. Thus, similarly to the present study, seagrasses demonstrated significant influence on nutrient dynamics at the sediment/water interface (Bulmer et al., 2018; Yarbro and Carlson, 2008).

It would be expected that, with the recorded dissolved oxygen concentrations, ammonium concentrations would decrease by its conversion into nitrates during the tidal period (Janas et al., 2019). The high NH_4 concentrations in the water column suggest the occurrence of bacterial decomposition in the sediment (Lillebø et al., 2006; Yarbro and Carlson, 2008), which promotes the release of this compound through the remineralization of organic matter (Janas et al., 2019; McGlathery et al., 2012). The ammonium and oxygen coexistence was possibly achieved through the occurrence of continuous fluxes between the sediment and the water column at vegetated sites. Nevertheless, primary production of other organisms such as microphytobenthos may justify higher oxygen concentrations and decreased NO_x and NH_4 concentrations (Janas et al., 2019).

In the present study, NO_x concentrations were always higher than NH_4 concentrations, both in intertidal pools and flux chambers, except in spring. Other authors (Bulmer et al., 2018; Qu et al., 2007) reported a reverse pattern with NO_x concentrations always lower than NH_4 concentrations, which can be attributed to distinct sediment characteristics such as OM content and O_2 concentration.

The lower NO_x concentrations in spring indicate the possible occurrence of denitrification (Eyre et al., 2011) and consequent release of N_2 to the atmosphere. NO_x variations found in the remaining seasons of the year, in the intertidal pools, may result from nitrification-denitrification processes occurring between the sediment and water column, as suggested by other authors (Eyre et al., 2011; Qu et al., 2007). On the contrary, in the flux chambers, no water column/atmosphere interface existed, and the NH_4 released from the sediment was significantly converted into NO_x, in the summer season.

In the case of phosphorus, results corresponded to the expected pattern, as there was an increase of PO_4 throughout the tidal cycle,

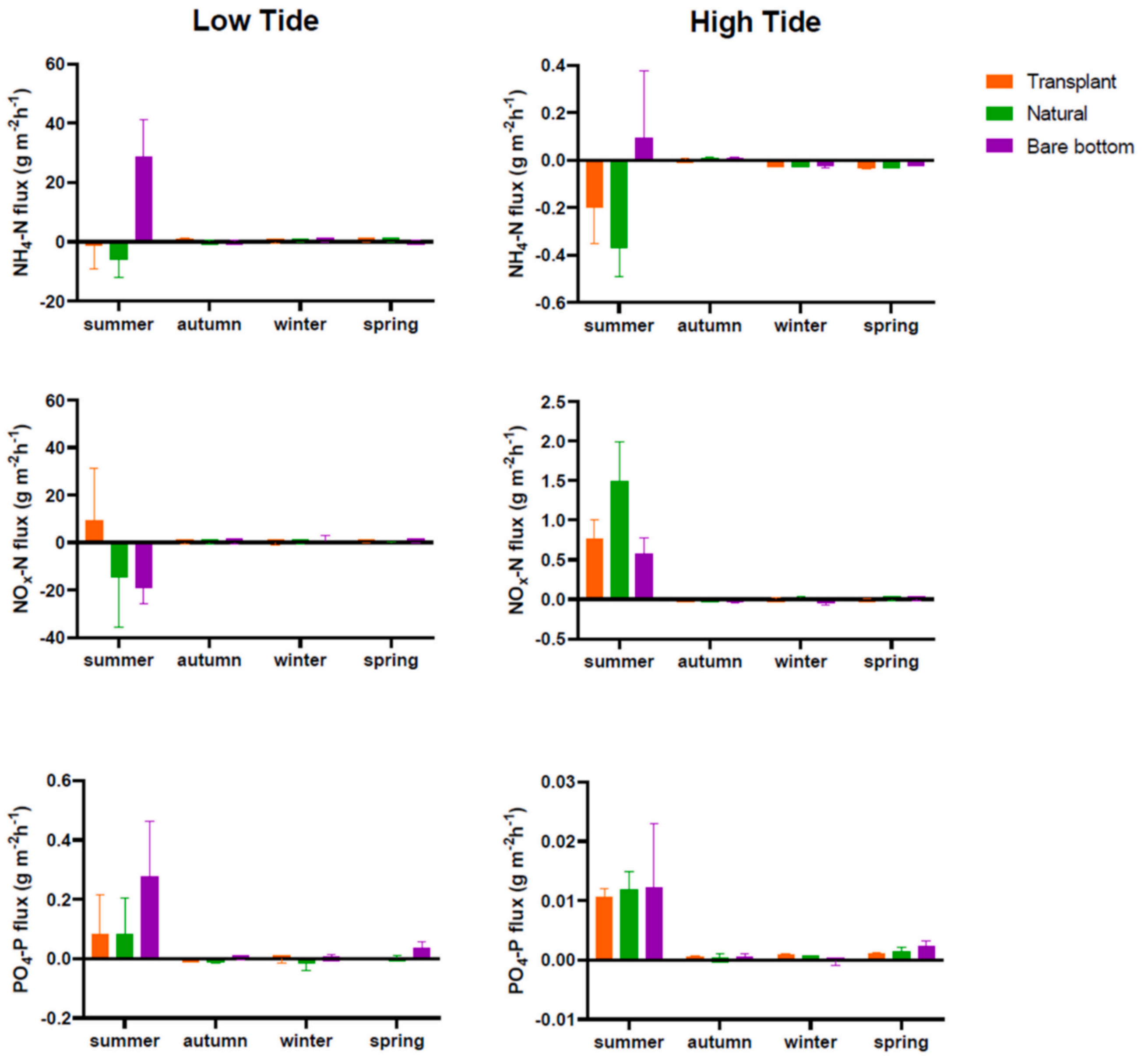

Fig. 4. NH_4-N, NO_x-N and PO_4-P fluxes (g m^{-2} h^{-1}) at each site, in each season, during low and high tide periods. All data is presented as mean ± standard error, $n = 3$.

coincident with an increase in temperature and decreased dissolved oxygen concentrations, especially in the adjacent unvegetated site. The obtained results are in agreement with Lillebø et al. (2004) reporting that the rapid increase in temperature and oxygen depletion in the intertidal pools leads to a PO_4 flux into the water column (Table 2). This behavior demonstrates the clear response of phosphorus to temperature variations, these results being in accordance with what is known and expected from other sites and/or systems.

In intertidal pools, increased temperatures and oxygen depletion stimulate orthophosphate flux, especially in summer, during the day. Absorption of phosphorus by plants for their growth and high adsorption capacity of the sediment in plants' oxidized rhizosphere may promote a decreased P flux from the sediment into the water column (Lillebø et al., 2002).

In autumn and winter, a period when the nutrient requirements of plants are reduced (McGlathery et al., 2004), phosphorus fluxes were minimal, that is, its concentrations remained approximately constant. This stability may be due to the lower temperatures recorded and reduced plant activity (Lillebø et al., 2002), the fluxes being similar in the vegetated and adjacent unvegetated sites, at this time of the year. In spring, some release could be considered, but when compared to summer season, concentrations can still be considered low. Lillebø et al. (2006) reported that seagrass species increase nutrient sequestration for growth purposes and promote rhizosphere oxidation, justifying the lower concentrations of orthophosphates in the interstitial water. Therefore, the rhizosphere oxidation promotes the uptake of orthophosphates by iron oxides and inhibits the release of this compound into the water column (McGlathery et al., 2004). Similar PO_4 fluxes from the

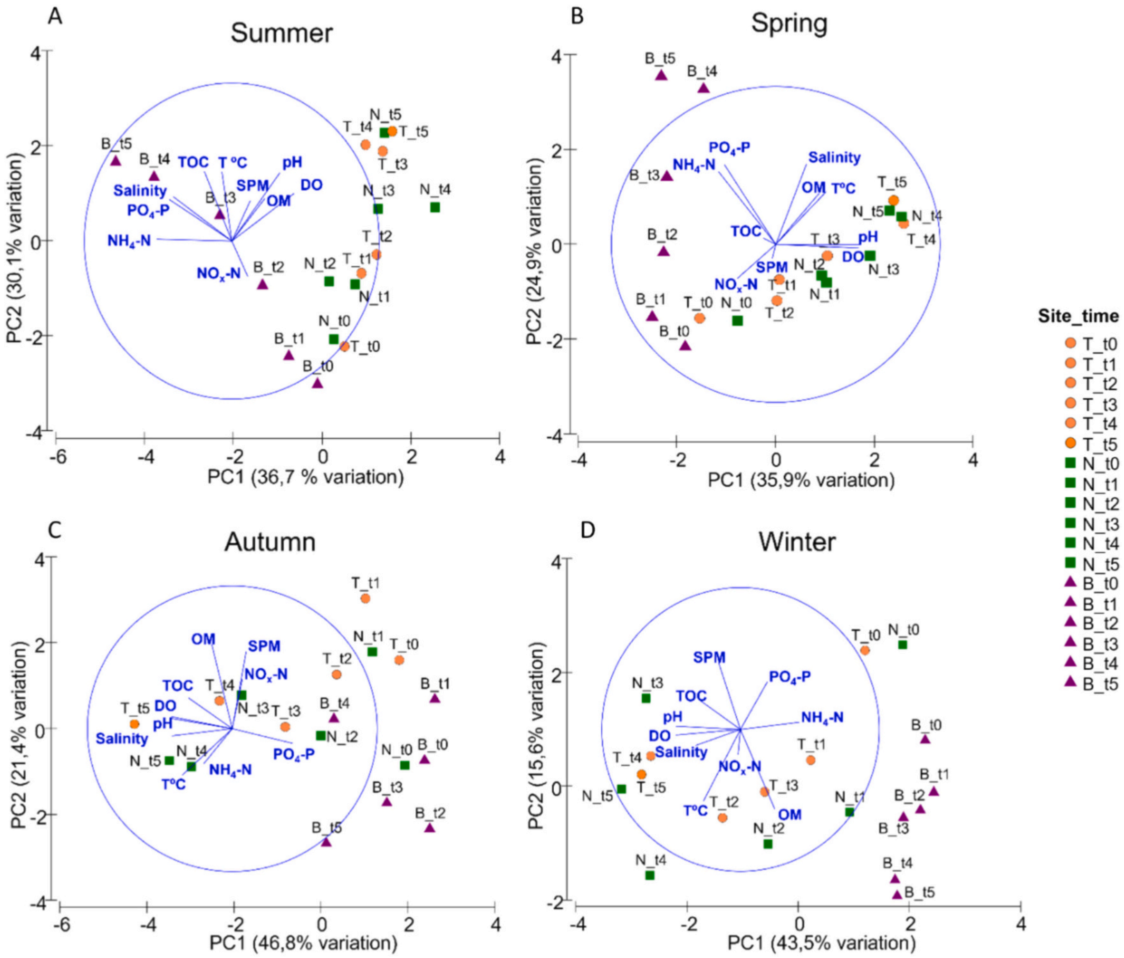

Fig. 5. PCA of experimental data for Summer (A), Spring (B), Autumn (C) and Winter (D).

Table 2
Comparative studies conducted on inorganic nutrient dynamics within different habitat/species and environmental compartments.

Location	Target	Experimental design	Environmental compartments	Habitat/ species	Relevant findings	References
Laranjo Bay Portugal	Dissolved Inorganic Nutrients (NH_4-N, NO_x-N, PO_4-P)	Seasonal Tidal cycle Circadian cycle	Water column Sediment	Seagrass *Zostera noltei* Bare Bottom	"… the presence of seagrasses, in the present work, inhibited the release of the analyzed compounds (…) reinforcing the influence of seagrass beds on nutrient dynamics at the sediment/water interface."	Present study
Mondego Estuary Portugal	Phosphorus concentrations	Tidal cycle Seasonal	Water column Sediment	Salt marsh *Spartina maritima* Seagrass *Zostera noltii* Bare bottom	"… seasonal/annual P-effluxes show that an eventual colonization of bare bottom mudflats by one of the three most common species in warm temperate estuaries (*Zostera noltii*, *Spartina maritima* and *Scirpus maritimus*) may reduce phosphate internal loading…"	Lillebø et al. (2004)
Arcachon Bay France	Dissolved Inorganic Phosphorus	Seasonal Inter-annual	Sediment	Seagrass *Zostera noltii* Bare Bottom	"… seagrass meadow decline represent an additional and significant input of phosphorus into the water column…"	Delgard et al. (2013)
Lake Illawarra Australia	Dissolved Inorganic Nitrogen (DIN)	Seasonal Circadian cycle	Water column	Seagrass *Ruppia megacarpa* Bare Bottom	"… nutrient fluxes displayed typical diel variations (…) suggesting the influence of benthic production on benthic nutrient fluxes …" "… unvegetated sediments displayed net DIN effluxes, while seagrass beds showed a net DIN uptake…"	Qu et al. (2007)

sediment into the water column were obtained at the three sites during high tide in summer season, possibly related to this mechanism, since dissolved oxygen concentration was reduced and similar between sites; probably leading to greater solubilization rates and PO_4 release from the sediment. These results are in accordance with Lillebø et al. (2006) which suggests that *Zostera* meadows significantly contribute to the orthophosphates efflux from the sediment at night. Still, low tide PO_4 fluxes (NO_x and NH_4 also) were always significantly higher than high tide situations when the effect of temperature is minimized.

Janas et al. (2019) investigated soft sediments inhabited by *Z. marina* in a coastal zone located in the southern Baltic Sea, and reported that aerobic conditions at the sandy sediment/water interface result in the adsorption of orthophosphates, removing this compound from the water column. In addition, high sequestration rates were observed by the sediment in the study area (Janas et al., 2019), demonstrating the influence of seagrass meadows over the availability of orthophosphates in the sediment and overlying water column. In turn, Delgard et al. (2013) and Qu et al. (2007) detected lower concentrations of dissolved inorganic phosphorus in vegetated sites, compared with unvegetated ones (Table 2). Additionally, Delgard et al. (2013) found that seagrass meadows decline represents an additional and significant source of phosphorus for the water column in that study area, highlighting, once more, the influence of seagrasses on the nutrient dynamics of the environment in which they occur (Delgard et al., 2013), as observed in the present study (Table 2).

Overall, the Principal Component Analysis showed that, in the period of greatest plant activity (spring-summer), the transplanted meadow was similar to the natural meadow, and these sites' similarity was mainly related to physico-chemical parameters (in turn, influenced by plant presence). In turn, the adjacent area without vegetation diverged from the vegetated sites during the tidal cycle, associated with the nutrient concentrations in the same period. On the other hand, in the period of lower plant activity (autumn-winter), a greater dispersion of the sites was observed and the difference between vegetated and non-vegetated sites was not evident, highlighting the significant effect of seasonal plant activity on the biogeochemistry of sediments and the water column.

Seagrass restoration success is usually assessed through measures of seagrass coverage and biomass (Oliveira et al., 2025). The path and pace of ecosystem functions recovery, however, is still largely unknown and requires clarification. All evidence from the present study supports the hypothesis that the nutrient regulation ecosystem function is efficiently recovered (less than one year) following seagrass restoration, considering the similar effect of restored and natural seagrass meadows on the seasonal nutrient fluxes. Similar findings were observed regarding contaminant porewater profiles, with a 40 % reduction in reactive/labile Hg reported three months after transplantation and similar to natural meadow (Oliveira et al., 2023). Both studies highlight the critical role that *Z. noltei* plays in sediment biogeochemistry, even before complete coverage is achieved, and may therefore be considered as an alternative/complementary measure of restoration success.

5. Conclusion

The transplant restored area was shown to be closer to the natural meadow than to the unvegetated adjacent area, since its behavior, in terms of ecosystem functions – nutrient dynamics, including fluxes, oxygenation and acidity control of the water column – was mostly equal to that of the natural meadow. The results obtained for nutrient fluxes in the transplant area were always closer to those of the natural meadow, allowing to conclude that the interactions in the rhizosphere, and consequent exchanges between the sediment and the water column, were reestablished in the transplanted area.

Additionally, the presence of seagrasses, in the restored area, inhibited the release of the analyzed compounds (NH_4-N, PO_4-P) from the sediment to the water column, reinforcing the influence of seagrass beds on nutrient dynamics at the sediment/water interface. Also, vegetated sites showed higher concentrations of O_2 and reduction of water acidity, demonstrating the regulatory effect that these marine angiosperms have in the environment in which they occur. The seasonal pattern of plant activity was also highlighted, as in the autumn-winter period, the vegetated area behavior was much closer to that of the adjacent bare sediment, while in the spring-summer period there was a greater differentiation.

In Largo do Laranjo, recolonization with *Zostera noltei* seagrass allowed the reestablishment of the process (e.g. uptake of nutrients), and function (e.g. nutrient dynamics specifically at the rhizosphere) of this ecosystem with regards to nutrient fluxes regulation, only one year after transplantation. This highlights the fast recovery of biogeochemical ecosystem process and functions, extremely important when it comes to implementing restoration measures.

This study contributes to showcase and reenforce the significant role of worldwide seagrass meadow restoration to achieve the internationally established objectives – SDG, UN, OSPAR, CBD, EU Green Deal – to combat climate change, ensure food security, improve water quality, and promote biodiversity.

CRediT authorship contribution statement

Raquel Fradoca: Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation. **V.H. Oliveira:** Writing – review & editing, Methodology, Investigation, Formal analysis. **B.A. Fonte:** Investigation. **A.I. Sousa:** Writing – review & editing, Resources, Methodology, Investigation, Formal analysis. **B. Marques:** Investigation. **A.I. Lillebø:** Writing – review & editing, Supervision, Resources, Methodology. **J.P. Coelho:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2025.117901.

Data availability

Data will be made available on request.

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