Salinity mediates ecosystem impacts of an invasive macrophyte across an aquatic continuum

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Abstract:

The ecological impacts of invasive species are increasingly recognized as context-dependent, yet the role of environmental gradients in shaping these effects remains poorly understood. This is particularly relevant in transitional aquatic ecosystems, where salinity gradients can constrain plant performance and alter ecosystem functioning. We investigated how salinity influences the functional role of the invasive macrophyte *Pontederia crassipes* by quantifying growth, nutrient uptake, and decomposition dynamics across a freshwater–marine continuum. Using a combination of mesocosm experiments (0–5 g L^{-1}) and *in-situ* litterbag assays along a natural salinity gradient (0–32 g L^{-1}), we assessed how key processes linked to ecosystem functioning vary across environmental conditions. We found that plant growth and nutrient uptake declined with increasing salinity, whereas decomposition rates increased markedly along with the gradient. These contrasting responses indicate a shift in the functional role of the species, from nutrient retention in freshwater systems to enhanced nutrient release under more saline conditions. Our results demonstrate that environmental gradients strongly modulate the ecosystem impacts of invasive macrophytes, highlighting salinity as a key driver of transitions between ecosystem service provision and ecosystem degradation. This context dependency has important implications for predicting invasion impacts and for managing transitional aquatic ecosystems.

Keyword: *Pontederia crassipes;* mesocosm; decomposition; invasive alien species; ecosystem service; disservice.

1 Introduction

Freshwater ecosystems represent approximately 0.01% of the global water volume (Dudgeon et al., 2006) and less than 1% of the global surface area (Mittermeier et al., 2011). Nevertheless, they play a

paramount role in supporting biodiversity and ecosystem services, including primary productivity and nutrient dynamics (Wantzen et al., 2016). Ecosystem services (ES) are defined as the benefits that humans derive from ecological processes, such as nutrient retention, sediment stabilization, and support for aquatic biodiversity (Costanza et al., 1997; MA, 2005). Aquatic plants are known to provide at least 24 different ES (Thomaz, 2023) under provisioning, regulation, and cultural categories.

Despite their ecological importance, freshwater environments are under increasing threat from multiple pressures (Borgwardt et al., 2019), such as biological invasions by alien species (Bellard et al., 2022), including aquatic plants. Biological invasions are caused by organisms that are introduced, either intentionally or unintentionally, in ecosystems outside of their native range. These organisms can then establish and spread, causing ecological and economic harm (Tasker et al., 2022; Diagne et al., 2021). According to the Wetland Global Assessment, invasions are the main cause of biodiversity loss in wetlands (Convention on Wetlands, 2025). Besides biological invasions, freshwater systems suffer from eutrophication symptoms, which are driven by excessive nutrient enrichment, particularly of nitrogen and phosphorus (Geletu et al., 2023). Together, biological invasions and eutrophication can drastically alter the structure and function of aquatic ecosystems. Macrophytes, with a central role in freshwater ecosystems by contributing to primary production and habitat provisioning (Thomaz & Cunha, 2010; Evangelista et al., 2014), can, conversely, generate ecosystem disservices, which refer to ecological processes or organisms that result in negative consequences for ecosystems or human well-being. Relevant examples of disservices include oxygen depletion, particularly at night when respiration is not compensated by photosynthesis, increased biomass clogging waterways, and competitive exclusion of native flora (Villamagna & Murphy, 2010).

One of the most widespread and ecologically impactful invasive macrophytes is *Pontederia crassipes* (Mart.), Solms also known as *Eichhornia crassipes* (Mart.) Solms, a name now acknowledged as a synonym (Pellegrini et al., 2018). This free-floating aquatic plant is native to South America and has spread to freshwater bodies across five continents (Téllez et al., 2008). *P. crassipes* can absorb large amounts of nitrogen and phosphorus, this contributes to its rapid growth, vegetative reproduction, and capacity to adapt to temperatures of 28–30 °C (Henares & Camargo, 2014; Wilson et al., 2005). It can also tolerate salinity concentrations of up to 6 g L^{-1} (Ghoussein, et al., 2023). These capabilities have been demonstrated under mesocosm experiments, including growth at different phosphorus concentrations (Kobayashi et al., 2008), greywater phytoremediation (Azabo et al., 2024), and biomass control under chemistry applications (Almeida et al., 2016). A remarkable growth rate 6.4% to 7% (doubling time of 9.6 to 10.8 days, respectively) was verified in eutrophic waters of the Rawapening Lake in Indonesia (Prasetyo et al., 2021).

Despite the extensive documentation of its growth and phytoremediation capabilities, significant knowledge gaps remain regarding the role of *P. crassipes* in nutrient dynamics along the aquatic continuum, from freshwater systems to estuarine and marine environments. Specifically, its dual role in nutrient uptake in upstream regions and potential nutrient release in downstream regions in an assimilatory-dissimilatory mechanism (Guitierrez et al., 2014), remains unclear. It is essential to understand how *P. crassipes* responds to a salinity gradient, particularly in the current and future contexts of increased saltwater intrusion in coastal

areas, contributing to assess its impact on nutrient dynamics and to develop effective ecosystem management strategies.

The Ria de Aveiro, a coastal lagoon in the Atlantic coast of Portugal that holds the estuary of the Vouga River, its main freshwater source, is a great example of an aquatic continuum covering freshwater, estuarine and marine environments. This classified area has been the subject of extensive socio-ecological and economic studies under the Natura 2000 network due to its high economic and environmental significance (Lillebø et al., 2019). The species *Pontederia crassipes* has been present in the Ria de Aveiro lagoon watershed since the early 20th century (Laranjeira & Nadais, 2008), exhibiting a seasonal pattern whereby it predominates in freshwater habitats for much of the year, moving towards more saline areas in autumn when river flow increases following rainfall (Fig. 1). Therefore, studying this species in such a temperate coastal system provides an ideal opportunity to investigate its response to salinity gradients and assess its potential influence on nutrient dynamics across from the freshwater to marine continuum.

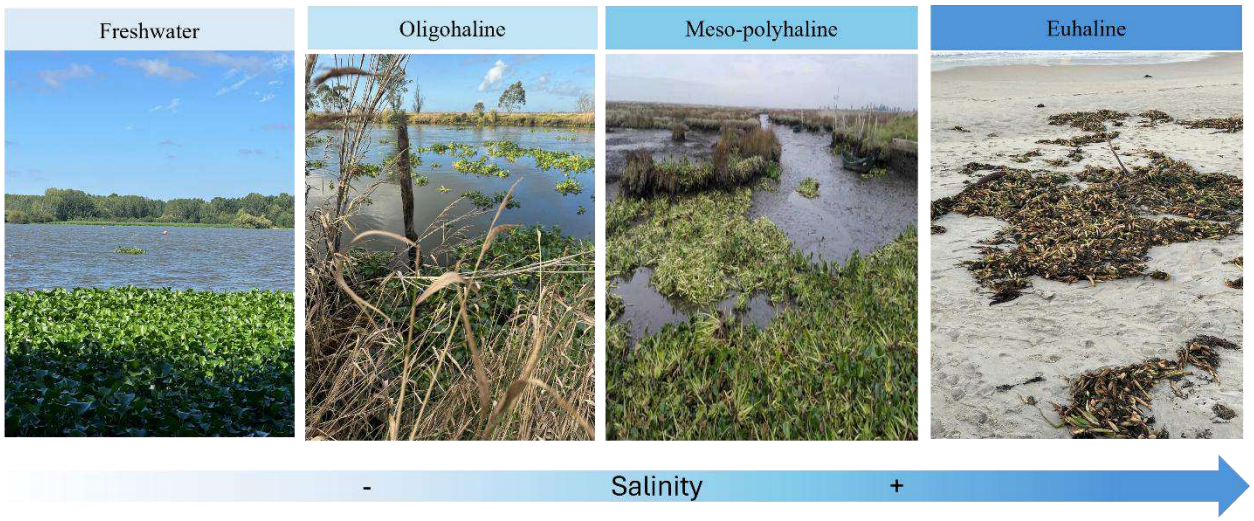

Fig 1: *Pontederia crassipes* across the salinity gradient from the freshwater (Pateira de Fermentelos lagoon; part of the Vouga River basin) passing through the lagoon brackish waters (Vouga River estuary) to the coastal euhaline waters ending up as beach wrack (Barra Beach).

This study was driven by the research question - What is the role of *P. crassipes* in nutrient dynamics along an aquatic salinity gradient across the freshwater–brackish continuum? Therefore, having Ria de Aveiro as showcase, this study aims to elucidate the role of *P. crassipes* in the nutrient dynamics of coastal aquatic ecosystems, with a focus on its dual function of nutrient uptake and potential release from decomposition across the Vouga River aquatic continuum, i.e., from more upstream freshwater to downstream estuarine waters. To this end, two hypotheses were identified: (i) the growth of different organs of *P. crassipes* and its capacity for nutrient uptake are significantly influenced by salinity along the freshwater–brackish gradient; and (ii) the decomposition rate of *P. crassipes* and the associated release of nutrients are significantly affected by salinity across the aquatic continuum from freshwater to estuarine conditions. To test these hypotheses, two complementary experiments were conducted: (i) a 28-day *ex-situ* mesocosm experiments with *P. crassipes* under a salinity gradient ranging from <1 g L^{-1} to 5 g L^{-1}, to assess the effect of salinity on the growth of different plant organs and evaluate the impact on nutrient uptake; and (ii) a 92 day *in-situ* decomposition experiment, using the litter bag methodology, under a salinity gradient

ranging from <1 g L^{-1} to 32 g L^{-1}, to assess the effect of salinity on decomposition and evaluate its impact on nutrient release. Together, these experiments will complementarily contribute to a better understanding of the ecological impact of the invasive species *P. crassipes* along the freshwater- estuarine continuum.

2 Materials and Methods

Both e*x-situ* and *in-situ* experiments were initiated in autumn (November 2024) when plants were still abundant in the field but not flowering and just before the biomass naturally decreases. Specimens of *P. crassipes* were collected from Pateira de Fermentelos lagoon (40.343056°N, 8.305691°W) part of Ria de Aveiro watershed, to be used in two different experiments: an *ex-situ* mesocosm experiment, and an *in-situ* decomposition experiment.

The Ria de Aveiro system situated in Portugal's Centro-Region (Fig. 2) is a temperate coastal lagoon of high ecological and socio-economic importance, recognised as a Long-Term Socio-Ecological Research (LT_SER) platform. It encompasses the Vouga River estuary, creating a dynamic interface between freshwater and brackish environments. The impact of invasive species on freshwater habitats, such as the Pateira de Fermentelos lagoon, and on estuaries and the sea has been demonstrated across this lagoonal system (Luis et al., 2025 and Laranjeira & Nadais, 2008).

The *ex-situ* mesocosm experiments were conducted in a greenhouse facility at ECOMARE – Laboratory for Innovation and Sustainability of Marine Biological Resources of the University of Aveiro. The *in-situ* litter bag experiment took place in selected sites along the aquatic continuum (Fig. 2). Experimental sites were chosen for their accessibility to minimise the risk of material loss during the experiment. The oligohaline sites (Site 1: 40.6950702° N, 8.6249475° W; Site 2: 40.6952281° N, 8.6013598° W) had low salinity of 0.34 ± 0.63 and 1.3 ± 1.6 (mean ± sd), respectively. In contrast, the mesohaline/polyhaline and euhaline sites (Site 3: 40.6456448° N, 8.6634199° W; Site 4: 40.6379169° N, 8.729826° W respectively) showed salinities of 24.5 ± 6.0 and 31.4 ± 1.9 (mean ± sd) respectively, during the experiments.

For both experiments, the samples were placed in plastic bags and transported to ECOMARE laboratory, where they were carefully cleaned and weighted.

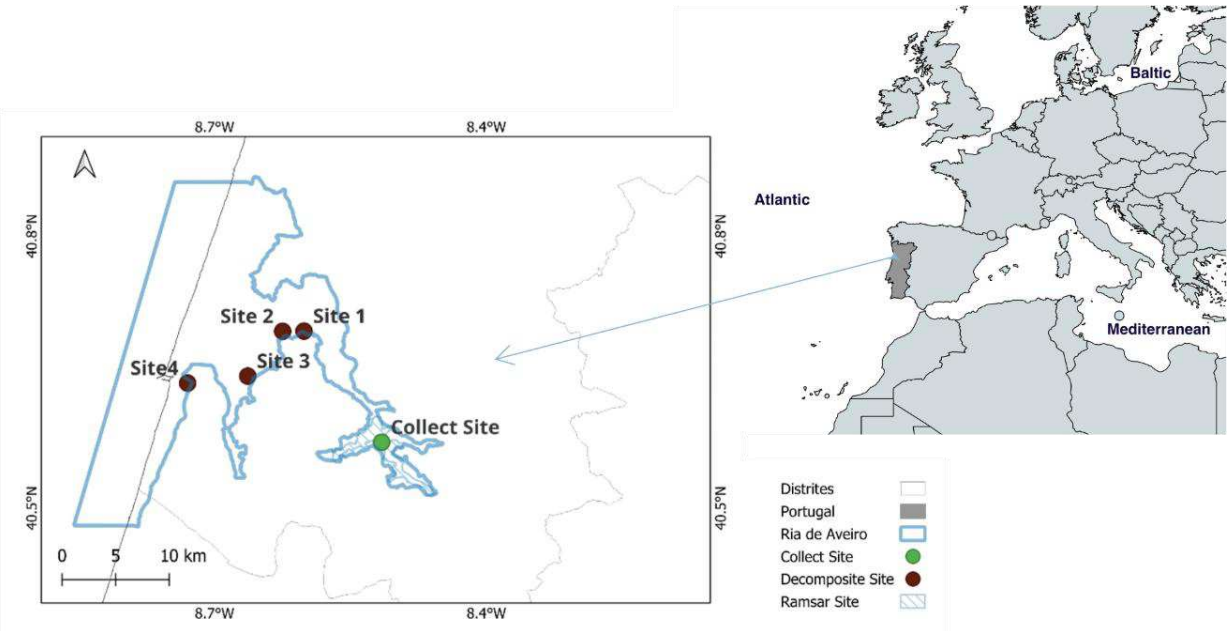

Fig. 2: Location of Ria de Aveiro with the delimitation of the area classified under Natura 2000. The detailed map depicts the area where *P. crassipes* was collected (at Pateira de Fermentelos lagoon) and the sites selected for the decomposition experiment along the aquatic continuum, from freshwater/oligohaline (Site 1) to the euhaline habitat (Site 4). Wider biogeography map built with mapchart.net.

2.1 Mesocosm experiment

To verify the growth and nutrient uptake performance, we hypothesised that salinity along the freshwater–brackish water gradient significantly affects the growth and nutrient uptake of *P. crassipes*. Specifically, we tested the null hypothesis (H_0) that there are no significant differences in biomass growth and nutrient uptake rates across the aquatic continuum under mesocosm conditions. In the *ex-situ* experiment we used 20 plastic containers (400 × 300 × 243 mm; see Fig. 3), each containing 15 L of Hoagland solution and stocked with three healthy water hyacinths (average fresh biomass: 35.84 ± 12.81 g, mean ± sd), sourced from the Pateira de Fermentelos lagoon, and maintained under natural light and temperature (20.0 ± 1.9 °C, mean ± sd). The study was conducted in a greenhouse for a period of four weeks. Prior to the start of the experiment, plants were acclimated for one week in Hoagland solution. After that, the salinity treatments simulating natural gradients from freshwater (<1 g L^{-1}) to transitional waters (2, 3, and 5 g L^{-1}), were introduced. A completely randomized design was applied to standardize conditions across all treatments. Each mesocosm trial lasted 28 days, with a water residence time approximately 10 days. Half of the nutrient solution was renewed weekly (Custódio et al., 2021).

The growth medium was based on Hoagland's nutrient solution (Hoagland & Aron, 1950) modified for use in aquatic mesocosms (Brito et al., 2026). The preparation of the solution is detailed in Table 1.

Table 1: Adapted Hoagland Solution nutrients components as described in Brito et al., 2026.

Hoagland's Stock Solutions (SS)	Stock Solution Concentration	Volume SS in Final Hoagland Solution
Macro nutrients SS		
1	1.00M $NH_4H_2PO_4$	1ml/L
2	1.00M KNO_3	6ml/L
3	1.00M Ca $(NO_3)_2$ $4H_2O$	4ml/L
4	1.00M $MgSO_4 \cdot 7H_2O$	2ml/L
Micronutrient SS		
5	2.86g H_3BO_3 /1L	1ml/L
	0.08 g $CuSO_4.5$ H_2O /1L	
	0.22g $ZnSO_4 \cdot 7H_2O$ /1L	
	1.81g $MnCl_2$ /1L	
	0.02g H_2MoO_4 /1L	
Iron stock		
6	26.1g EDTA /1L	0.25ml/L

Each experimental unit consisted of three plants, and a total of 20 units were used, corresponding to five replicates per setting: one control (freshwater with salinity <1 g L^{-1}) and three different concentrations of salinity (2, 3, and 5 g L^{-1}) (Fig. 3). Artificial seawater was prepared by dissolving Red Sea® salt (Red Sea, Cheddar, UK) in Hoagland solution, which was made with reverse osmosis-purified tap water (V2 Pure 360 RO System, TMC, Hertfordshire, UK).

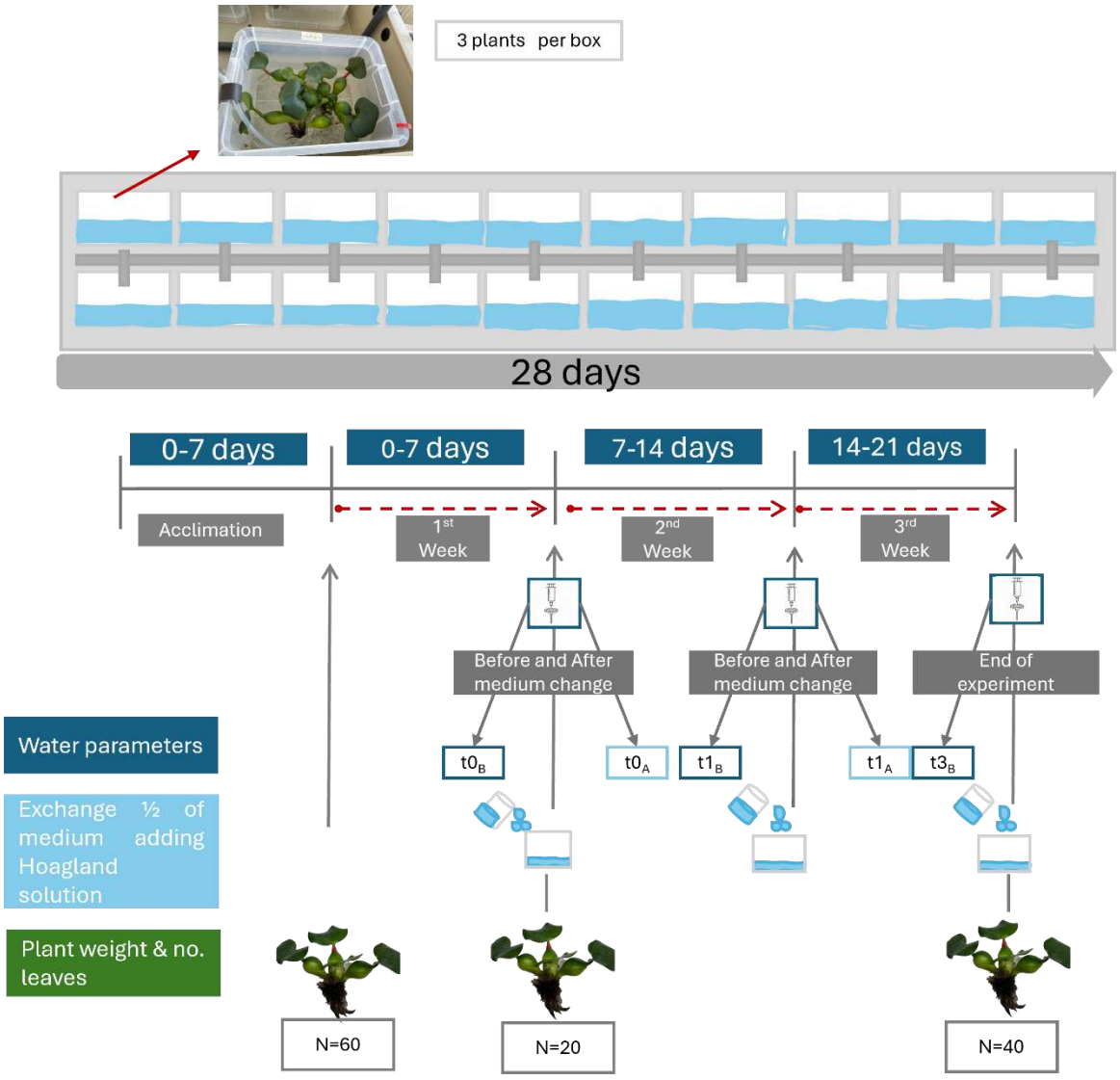

Fig. 3: Experimental design. Mesocosm experiments were conducted with *P. crassipes* under Hoagland and different salinity conditions in a greenhouse at ECOMARE in Aveiro, Portugal.

2.1.1 Water analyses

Water samples (0.2 L) were filtered through 0.47 µm membranes (Custódio et al., 2021) before and after changing half of the volume of the solution in the boxes, every week (weeks 1, 2 and 3 of the experiment) (Fig. 3). The filtered samples were frozen at -20°C. pH was measured using a portable multiparameter meter (ProfiLine pH/Cond 3320, WTW, Germany), and dissolved oxygen was assessed with a portable oxygen meter (Oxi 3310, WTW, Germany). Concentrations of dissolved inorganic nutrients, namely ammonium (NH_4-N), nitrogen oxides (NO_x-N), and orthophosphate (PO_4-P), were determined using a Skalar San++ continuous flow analyzer (Skalar Analytical, Netherlands). Dissolved inorganic nitrogen (DIN-N) was calculated as NH_4-N + NO_x-N, while dissolved inorganic phosphorus (DIP-P) was equal to PO_4-P.

2.1.2 Biomass measured

Biomass was quantified by measuring the fresh weight of *P. crassipes* over a four-week experimental period. Measurements were taken at the start of the acclimation stage (Day 0), one week after the addition of salinity (Day 7), and at the end of the second (Day 14) and third (Day 28) weeks of the experiment. All samples were weighed using an analytical balance.

Total biomass

The average fresh biomass for each *P. crassipes* plant was 35.6 g ± 12.81 (mean ± sd).

Liquid productivity

The liquid productivity growth was calculated as the difference between fresh biomass at each sampling time (Day 7, Day 14 and Day 28) and the beginning (Day 0) divided by the corresponding time interval (days), according to the following expression:

Liquid productivity = (Fresh weight final- Fresh weight initial/ time).

Productivity was expressed daily.

Relative Growth Rate

The Relative Growth Rate (RGR, day^{-1}) was calculates from the total dry mass (DM), of the plant using the formula utilized by Hoffmann et al. (2002) (q. 2),

(Equation 2)

$$RGR = (\ln M_n - \ln M_n\text{-}1) * t^{-1}$$

where:

- M_n is total dry mass at the current sampling,
- M_{n-1} is total dry mass at the previous sampling,
- t is time in days between samplings.

During the acclimatisation period, dry mass (DM) was estimated from fresh mass (FM) using a conversion factor of 0.05 (Penfound & Earle, 1948) to avoid destructive sampling. Once the treatments had begun, the dry mass of the plants was determined gravimetrically at each sampling event, revealing temporal variation in the DM:FM ratio. Consequently, all final RGR values reported in this study were calculated using dry mass measured experimentally.

2.2 Decomposition experiment

To evaluate the role of *P. crassipes* in nutrient cycling via the decomposition of downstream biomass, we tested the null hypothesis (H_0) that there are no significant differences in decomposition rates

across the aquatic continuum, using a litter bags methodology. The litter bags (50 cm x 30 cm), made from 5 mm mesh and containing 50g of fresh plant biomass each, were deployed at four locations: one freshwater and one oligohaline water, both in the Vouga River (Site 1 and Site 2), one in mesohaline/polyhaline waters (Site 3), and one in the euhaline (Site 4) (Fig. 2). The Venice System classification, as reported by Vaz & Dias (2011), was used to classify the sites under the Ria de Aveiro system of lagoons. Before placing the litter bags in the water, we mechanically damaged the floating nodules in the stems of the water hyacinths to prevent them from floating.

There were three replicates at each site at six sampling times (3, 7, 15, 30, 60 and 92 days), plus time zero. Unfortunately, there is no data for Site 4 for days 60 and 92, as the units were lost due to strong hydrodynamics or local fishing activity. For this reason, we divided the analyses into two groups: after 30 days (four sites) and after 92 days (three sites). The decomposition rates were modelled using the exponential decay equation of Olson (1963):

(Equation 3)

$$W_t = W_0 \cdot e^{-kt}$$

where:

- t is time (days),
- W_t is litter mass at time t,
- W_0 is the initial mass (100%),
- k is the decomposition rate constant (day^{-1}),
- e is the base of the natural logarithm.

Since the decomposition experiment used fresh biomass, apparent biomass gains could potentially be observed. To account for this effect, a correction factor was applied. Specifically, ten plants were collected from the same site, weighed fresh, oven-dried at 65 °C for until stabilize the weight, and weighed again to determine dry mass under the local conditions. On average (n = 10), dry matter represented 11% of total fresh biomass, with water accounting for the remaining 89%. Accordingly, all biomass values were converted to dry mass by multiplying fresh biomass by 0.11 prior to analysis. All graphical representations and statistical analyses were therefore conducted using dry biomass values.

To standardise biomass trajectories and avoid misleading interpretations of early apparent biomass gain, the fraction of dry biomass remaining at each sampling time (Fraction) was calculated as the ratio between dry biomass at time $t(B_t)$ and the initial dry biomass (B_0):

(Equation 4)

$$\text{Fraction} = \frac{B_t}{B_0}$$

Values equal to 1 indicate maintenance of biomass, whereas values below 1 indicate net biomass loss. This normalised fraction was used in all subsequent analyses and graphical representations. To explore potential phase transitions in decomposition dynamics, breakpoints were initially estimated using segmented regression to identify changes in temporal trends. Given the limited temporal resolution and associated uncertainty in breakpoint estimation, breakpoint analyses were used as exploratory support. For graphical representation and comparative purposes, day 7 was used as a common reference point corresponding to the onset of net biomass loss, based on visual inspection and ecological reasoning (Fig. 8). All models were implemented within a mixed-effects framework to account for site-specific variability.

2.3 Statistical analyses

For the *ex-situ* mesocosm experiments, we statistically analysed water parameters oxygen content, temperature, conductivity and pH. For each parameter, measured in twelve independent groups, each with five replicates (n = 5), the group means and standard deviations were calculated, and an overall mean was obtained by averaging group means; variability was estimated using a pooled standard deviation (sd) of the standard deviations in each group, from which the standard error of the mean (SEM) and 95% confidence interval (CI) were derived assuming a t-distribution (df=59, 5 reps*12 groups).

To assess the effect of treatment over time, each of the above water parameters, plant and nutrients (DIN-N, DIP-P, NH_4^+-N and NOx-N) were analysed using a linear mixed-effects model fitted with the *lmer()* function from the *lme4* package (Bates et al., 2015). Treatment, Week and their interaction were included as fixed effects. To control for pseudo replication, Box was included as a random effect. Repeated measures analysis of variance (ANOVA) was used to test for significant effects, followed by a Tukey's post hoc test using the *emmeans* package (Lenth, 2019). For RGR, as the variance among boxes was negligible and the mixed-effects model failed to converge, a two-way ANOVA was fitted using a standard linear model lm(), with treatment, week, and their interaction as fixed factors.

For the decomposition experiment, to assess differences between sites, we performed a one-way ANOVA with a post hoc test for multiple comparisons. A complementary analysis focusing on the first 30 days was conducted to examine the initial phase of decomposition. However, the breakpoint analyses were conducted using piecewise linear models in *segmented* package (Muggeo, 2025). All results were presented graphically and grouped by time using the *ggplot2* package (Wickham, 2016).

Statistical analyses were performed in R version 4.4.3 software (R Core Team, 2025).

3. Results

3.1 Physico-chemical variations in water under *Pontederia crassipes* exposure to a salinity gradient

During the 28 days experiment, oxygen concentrations remained rather stable (Table 2), despite week 2 showing significantly higher mean values (9.98 mg/L) than the first and last weeks of the experiment (Fig. S1, Table S2). Nonetheless, observed values during the entire experiment were within adequate levels to support good ecological aquatic functions, with a (relatively small overall standard error (SEM = 0.08, n

= 60; Table S1) across all settings and mean oxygen concentrations laying between a narrow 95% confidence interval (CI) of 9.56 to 9.88 mg/L. Likewise, in week 2 water temperature significantly differed from the other periods, showing a slight decreased in mean values (14.6 ºC) (Fig. S2, Table S3). Nonetheless, temperature variation across settings was small (SEM=0.28; Table S1) and within expected ranges (Table 2) for the late autumn season in the system (95% CI from 15.45 to 16.56 °C; Table S1), indicating stable and well-controlled experiment conditions.

Table 2: Water parameters variation (mean ± sd) in *P. crassipes* whole plant mesocosm *ex-situ* experiment over a 3-Week period under different salinity exposure conditions (Treatment). † post-hoc Tuckey Test significantly different groups *(p<0.001)*

	Treatment	**Oxygen (mg/L)**	**Temperature (ºC)**	**Conductivity (µs/cm)**	**pH**
Week1	Control	9.53 ± 0.74	16.81 ± 3.07	1707.34 ± 881.69	3.83 ± 0.25
	Salinity2	9.47 ± 0.70	16.86 ± 3.02	3254.86 ± 191.69	4.29 ± 0.50
	Salinity3	9.53 ± 0.67	17.10 ± 3.04	4626.00 ± 393.01	4.68 ± 0.62
	Salinity5	9.54 ± 0.76	16.61 ± 3.06	7436.29 ± 502.66	5.29 ± 0.59
Week2	Control	9.98 ± 0.55†	14.68 ± 1.96†	1719.14 ± 151.48	3.79 ± 0.42
	Salinity2	9.95 ± 0.51†	14.62 ± 1.90†	3163.71 ± 143.84	4.11 ± 0.45
	Salinity3	9.96 ± 0.52†	14.93 ± 1.85†	4498.57 ± 218.98	4.40 ± 0.40
	Salinity5	10.03 ± 0.53†	14.31 ± 2.02†	7050.86 ± 350.66†	5.67 ± 0.72
Week3	Control	9.62 ± 0.58	16.49 ± 1.47	1847.23 ± 109.39	3.82 ± 0.21
	Salinity2	9.69 ± 0.55	16.49 ± 1.45	3290.86 ± 121.42	4.40 ± 0.63
	Salinity3	9.65 ± 0.53	16.84 ± 1.38	4686.57 ± 148.84	5.20 ± 0.43
	Salinity5	9.68 ± 0.54	16.34 ± 1.50	7446.00 ± 262.09	6.21 ± 0.14
Anova					
Treatment effect	F (df=3)	0.22 (p=0.88)	0.68 (p=0.578)	2035.70 **(p<0.001)**	42.65 **(p<0.001)**
Week effect	F (df=2)	27.60 **(p<0.001)**	40.65 **(p<0.001)**	13.21 **(p<0.001)**	43.91 **(p<0.001)**
Treatment:Week	F (df=6)	0.09 (p=0.99)	0.019 (p=1.0)	2.68 **(p=0.03)**	12.684 **(p<0.001)**

Conductivity and pH conditions differed significantly across salinity exposure conditions during the entire duration of the experiment, with increasing values observed at increasingly salinity conditions (Table 2 and Fig. 4). The salinity exposure treatment effect in conductivity was expected, and control conditions presented the lower mean conductivity values of 1757 µS/cm (Table 2), which in this experiment were higher than the normal range expected for freshwater conditions. The mean conductivity values for the exposure treatments across oligohaline conditions (2, 3 and 5 g L^{-1}) were respectively 3236, 4603 and 7311 µS/cm (Fig. 4), which were also higher than expected for brackish waters near the freshwater spectrum. During the experiment, conductivity conditions remained quite stable across all treatments, expect for week 2 in the higher exposure treatment (Table S4) where it showed a significant dip with respect to the values observed

in the previous and subsquent week (Fig. 4), but still with values above 7000 µS/cm (Table 2), higher than the other treatments.

For pH, during the entire duration of the experiment, a lower acidity pattern was generally observed with increasing salinity exposure, despite some overlap between treatment 2 and 3 during the first two weeks (Table S5), but still the mean pH was higher at the higher exposure (Table 2). Unlike the other water paramenters, for pH at the higher salinity exposure treatments (3 and 5 g L^{-1}) there was a significant difference between the starting conditions (at week 1) and the end of the experiment (in week 3), where pH values registered significant increases (Table 2). This increase was observed already in the second week for the highest exposure (Table S5; Fig. 4), and kept increasing significantly, until the end of the experiment; up to 5.20 ± 0.43 in exposure 3 g L^{-1} and in the highest exposure up to just slightly acidic conditions (6.21 ± 0.14), reaching the lower limit of the tolerable range for most aquatic life. In the control and in the lowest exposure treatment (2 g L^{-1}) no relevant pattern was observed (Table S5) and mean water conditions remained highly acidic across the entire experiment (mean treatment values around 3.8 and 4.3 respectively).

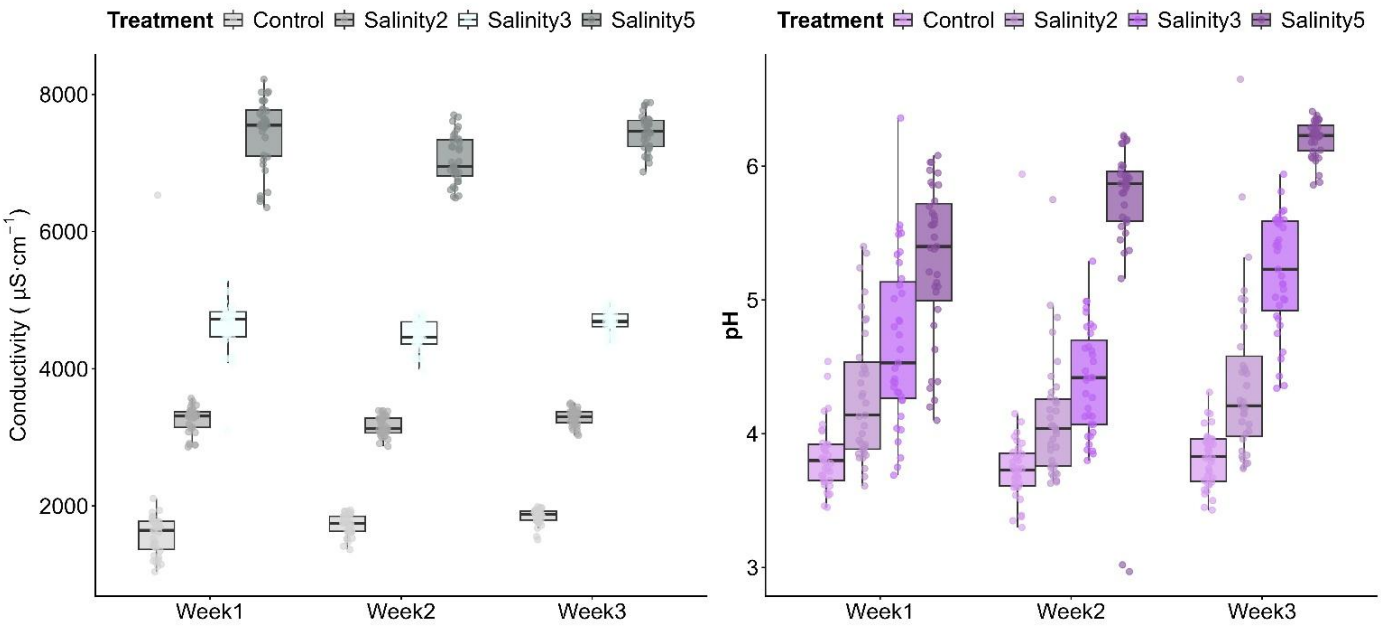

Fig. 4: Variation of conductivity and pH in *Pontederia crassipes* under salinity mesocosm experiment over the weeks.

3.2 Impact of salinity gradient on *Pontederia crassipes* leaf growth

During the experiment, new leaves were produced by plants, despite salinity exposure (Fig. 5). The increase in the number of leaves was significantly higher under control and lower salinity exposure (2 g L^{-1})

conditions with an average of 9.6 new leaves, representing an increase of 239% (Table S6). At intermediate exposure an average of 8.8 new leaves (220%) were observed while at the highest exposure treatment a significantly lower number of leaves were registered on average (5 leaves; 135%) to (Fig. 5). The maximum increase was observed in control conditions with 16 new leaves registered during the 3-week period, and the minimum of 1 new leaf was registered at highest salinity exposure (5 g L^{-1}) (Table S6).

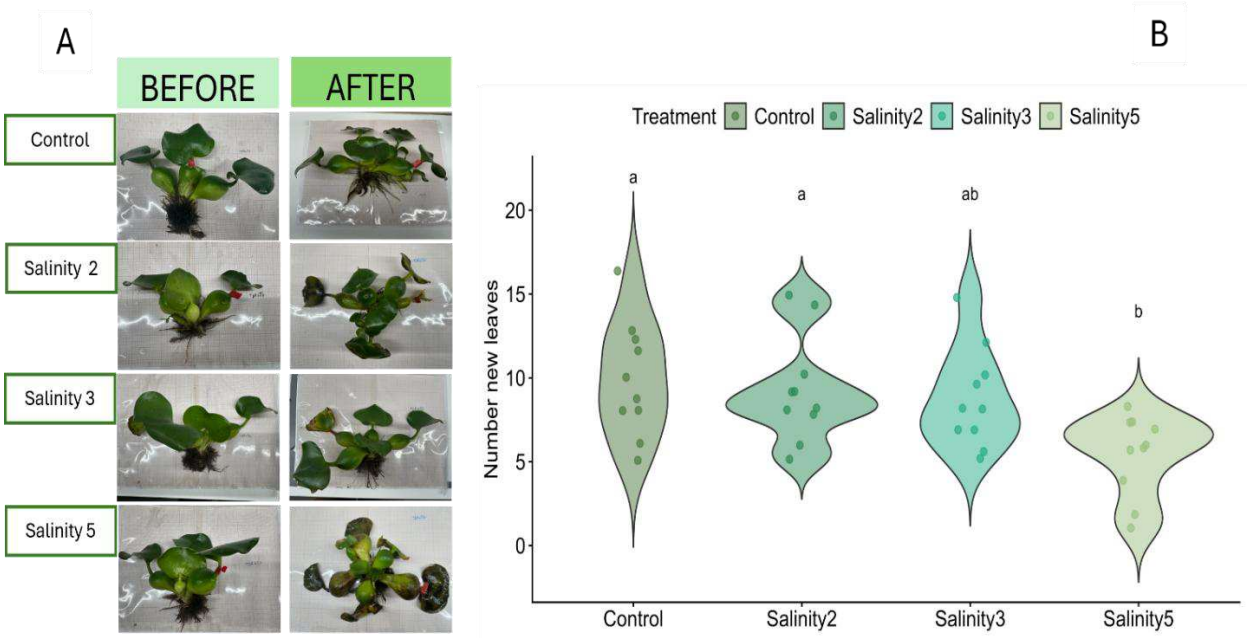

Fig. 5: (A) Visual representation of *Pontederia crassipes* before and after exposure to salinity treatments in the *ex-situ* mesocosm experiment. The images illustrate plant structure prior to treatment and at the end of the experimental period; (B) The number of leaves produced under different levels of salinity exposure. Letters indicate statistically significant differences across treatments.

Although, in this experiment, leaf emergence suggests slight tolerance of *P. crassipes* to salinity increase, plants at the highest salinity concentration (5 g L^{-1}) exhibited chlorosis within a few days (author personal observation during the course of the experiment; similarly to chlorosis observed in Fig. 5A photo taken at the end of the experiment from the two highest exposure treatments).

3.3 Potential growth of *Pontederia crassipes* along the aquatic continuum

Growth performance of *P. crassipes* under increasing salinity exposure was evaluated using three complementary measures. They indicate that, overall, the plant grew throughout the entire experimental period, but the performance was best under freshwater conditions decreasing with increasing salinity exposure.

By the end of the 28 days, total biomass had increased significantly in all treatments (Table 3). This growth is also reflected in the liquid productivity, i.e., the increase in fresh biomass divided by the number

348 of days, which presented positive values in most settings, indicating favourable growth conditions overall
349 (Table 3), expect for the highest exposure treatment where a decrease was observed during the first week
350 (Fig. 6). In fact, the liquid productivity shows a significant increase for all treatments towards the end of the
351 experiment (Table 3, Fig. 6), with control and consecutively lower salinity exposures growing faster with
352 time, i.e., with higher Liquid productivity rates than those observed for higher salinity conditions (Table S7).
353 The growth performance measured by the Relative Growth Rate (RGR), based on the plant dry weight,
354 indicates a constant growth over time rates (Table 3), including for the treatment with the highest exposure,
355 which showed the similar RGR rate in all treatments at the end of the experiment (Table S8).
356

Table 3: Mean and ANOVA results of biomass (fresh biomass in g), Relative Growth Rate (RGR g dw day^{-1}), and liquid productivity (g fw day^{-1}) of *Pontederia crassipes* under gradient salinity treatments during the experimental period. Values are shown as a mean and standard deviation (n as indicated), and significant results are highlighted in bold.

Time	**Treatment**	**n**	**Biomass total (g fw)**	**RGR (g dw day^{-1})**	**Liquid productivity (g fw day^{-1})**
Week 1	Control	5	46.87 ± 1.57	0.05 ± 0.01	0.96 ± 0.32
	Salinity2	5	45.03 ± 16.27	0.05 ± 0.01	0.59 ± 0.36
	Salinity3	5	49.07 ± 5.95	0.05 ± 0.02	0.66 ± 0.34
	Salinity5	5	41.13 ± 13.17	0.04 ± 0.01	-0.30 ± 0.26
Week 3	Control	10	69.72 ± 31.52	0.16 ± 0.02	1.24 ± 0.87
	Salinity2	10	73.81 ± 32.37	0.14 ± 0.02	1.29 ± 0.66
	Salinity3	10	69.78 ± 25.63	0.14 ± 0.02	1.04 ± 0.44
	Salinity5	10	78.69 ± 19.9	0.14 ± 0.01	0.72 ± 0.20
ANOVA					
Effect					
Treatment		F (df=3)	0.078 (p=0.971)	1.5593 (p=0.2104)	7.336 **(p<0.001)**
Time		F (df=1)	16.561**(p< 0.001)**	538.605 (p**<0.001**)	17.086 **(p<0.001)**
Treatment:Time		F (df=3)	0.312 (p=0.816)	1.2951 (p=0.2859)	1.315 (p=0.280)

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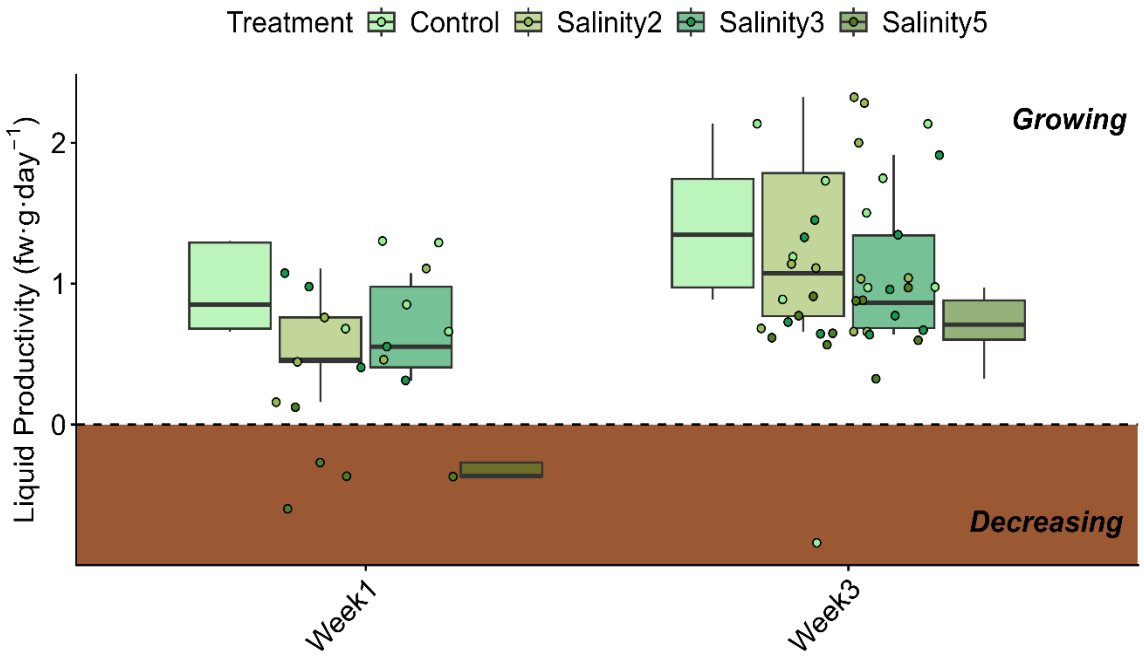

Fig. 6: Biomass liquid productivity of *Pontederia crassipes* under different salinities in an *ex-situ* mesocosm experiment.

3.4 Impact of salinity on nutrient uptake by *Pontederia crassipes*

Release or uptake of nutrients in water by *P. crassipes* varied markedly across salinity treatments and such patterns changed throughout the duration of the experiment (Fig. 7). The negative value represents the uptake of nutrients from water by plants. All nutrient concentration dynamics (DIN-N, DIP-P, NH_4^+-N and NO_x-N) were significantly affected by salinity and exposure time (Table 4; Supplementary Material Table S19-S12). Nonetheless the highest uptake or release concentrations were generally observed under higher and longer exposures (Fig. 7).

Table 4: Nutrients concentrations in water (mean ± sd) in *Pontederia crassipes* mesocosm experiment over the weeks under different salinity exposure. Significant results (*p*-values) in bold.

		DIN-N (mg/L)	**DIP-P(mg/L)**	**$NH4^+$-N (mg/L)**	**NO_x-N (mg/L)**
Initial concentrations a t0:		*224.60 ± 66.62*	*26.80 ± 6.57*	*9.02 ± 4.08*	*215.58 ± 66.01*
Treatment	**Week**				
Control	Week1	-1415.57 ± 1069.95	-19.07 ± 83.24	-11.51 ± 47.63	-1404.06 ± 1063.43
	Week2	431.46 ± 449.51	-80.26 ± 61.44	-31.43 ± 33.48	462.89 ± 431.92
	Week3	373.56 ± 1376.63	113.83 ± 54.39	49.54 ± 25.66	324.02 ± 1395.42

Salinity2	Week1	55.59 ± 941.73	-116.44 ± 96.21	-112.99 ± 72.22	168.58 ± 950.51
	Week2	798.34 ± 1633.35	-8.18 ± 99.92	-48.70 ± 44.23	847.04 ± 1610.93
	Week3	2408.51 ± 1406.46	186.19 ± 103.91	94.80 ± 37.03	2313.71 ± 1406.75
Salinity3	Week1	719.59 ± 973.46	105.18 ± 72.17	43.11 ± 53.42	676.48 ± 965.71
	Week2	39.04 ± 716.14	-52.92 ± 106.69	8.61 ± 37.77	30.42 ± 686.98
	Week3	577.73 ± 647.66	129.27 ± 105.34	53.91 ± 42.67	523.82 ± 653.97
Salinity5	Week1	-780.36 ± 607.79	-30.69 ± 57.56	-35.34 ± 26.72	-745.02 ± 624.39
	Week2	495.50 ± 1128.95	15.72 ± 43.99	-6.93 ± 32.24	502.43 ± 1124.58
	Week3	-64.50 ± 437.01	-190.65 ± 80.37	-111.82 ± 54.03	47.31 ± 478.16
Anova					
Effect					
Treatment	F(df=3)	5.13 **(p=0.003)**	6.30 **(p=0.001)**	10.40 **(p<0.001)**	5.09 **(p=0.004)**
Time	F (df=2)	6.95 **(p=0.002)**	6.82 **(p=0.002)**	7.48 **(p=0.001)**	6.45 **(p=0.003)**
Treatment: Time	F (df=6)	2.63 **(p=0.028)**	10.93 **(p<0.001)**	11.72 **(p<0.001)**	2.34 **(p=0.046)**

For Phosphorus, early in the experiment, conditions under control and low salinity exposure (2 g L^{-1}), there is a higher uptake or a net balance between release and uptake that changes significantly into a clear release pattern towards the end of the experiment (Fig 7; Table S9). At intermediate exposure (3 g L^{-1}) there is initially a DIP-P release pattern followed by an uptake and then again, a significant shift towards a release of Phosphorus. At the highest exposure, initial uptake is followed by a balance between release and uptake and then a significant change towards strong release of Phosphorus into water by the end of the experiment (Fig. 7; Table S9). For Ammonium, very similar patterns to those of Phosphorus were observed (Fig. 7), although trends were not always as expressive thus not all variations are significantly different (Table S10). Under control conditions and low salinity exposure (2 g L^{-1}) there is a shift from uptake to release towards the end of the experiment (Fig. 7; Table S10). At intermediate exposure (3 g L^{-1}) there is mostly an Ammonium release pattern trend. On the contrary, at the highest exposure, Ammonium uptake by the plant seems to dominate early on and significantly increase by the end of the experiment (Fig. 7; Table S10).

Regarding Nitrite+Nitrate N forms, overall, there was a tendency for the plant release to surpass its uptake (Fig. 7), with a few exceptions. In control conditions, there was initially a strong uptake that significantly changed towards a slight nutrient release pattern by the end of the experiment (Fig. 7; Table S11). At low exposure, the initial balance between uptake and release significantly changed towards a strong release of these nutrients in water by the end of the experiment. The release concentrations observed at low exposure by the end of the trial were significantly higher than those observed in any of the other treatments (Table S11). Dissolved nitrogen (DIN-N) release and uptake patterns by the plant were dominated by the contribution of Nitrite+Nitrate N forms (Pearson $r = 0.99$) and as such presented similar patterns (Fig. 7; Table S12) to the previously described.

Overall, for all nutrients, in Week 2, the differences in nutrients' absorption dynamics were minor across the treatments, possibly indicating the transient effects of salinity. In control conditions, nutrient

concentrations fluctuated, but nutrient uptake appeared to be the dominant pattern during the experiment moving towards a nutrient release pattern by the end of it (Fig. 7). Moderate salinity exposure appeared to initially enhance nutrient uptake, particularly of Phosphorus and Ammonium (Fig. 7), but prolonged exposure led to strong release of all nutrients tested. Moderate salinity exposure (3 g L^{-1}) promoted nutrients release from the beginning of the experiment, expect for Phosphorus in week 2 (Fig. 7). In contrast, the highest salinity treatment tended to cause strong absorption of Phosphorus and Ammonium (Fig. 7) by the plant, particularly in the end, while for the Nitrite and Nitrate N-dissolved forms a slight initial uptake was observed followed by release and net nutrient uptake towards the end (Fig. 7).

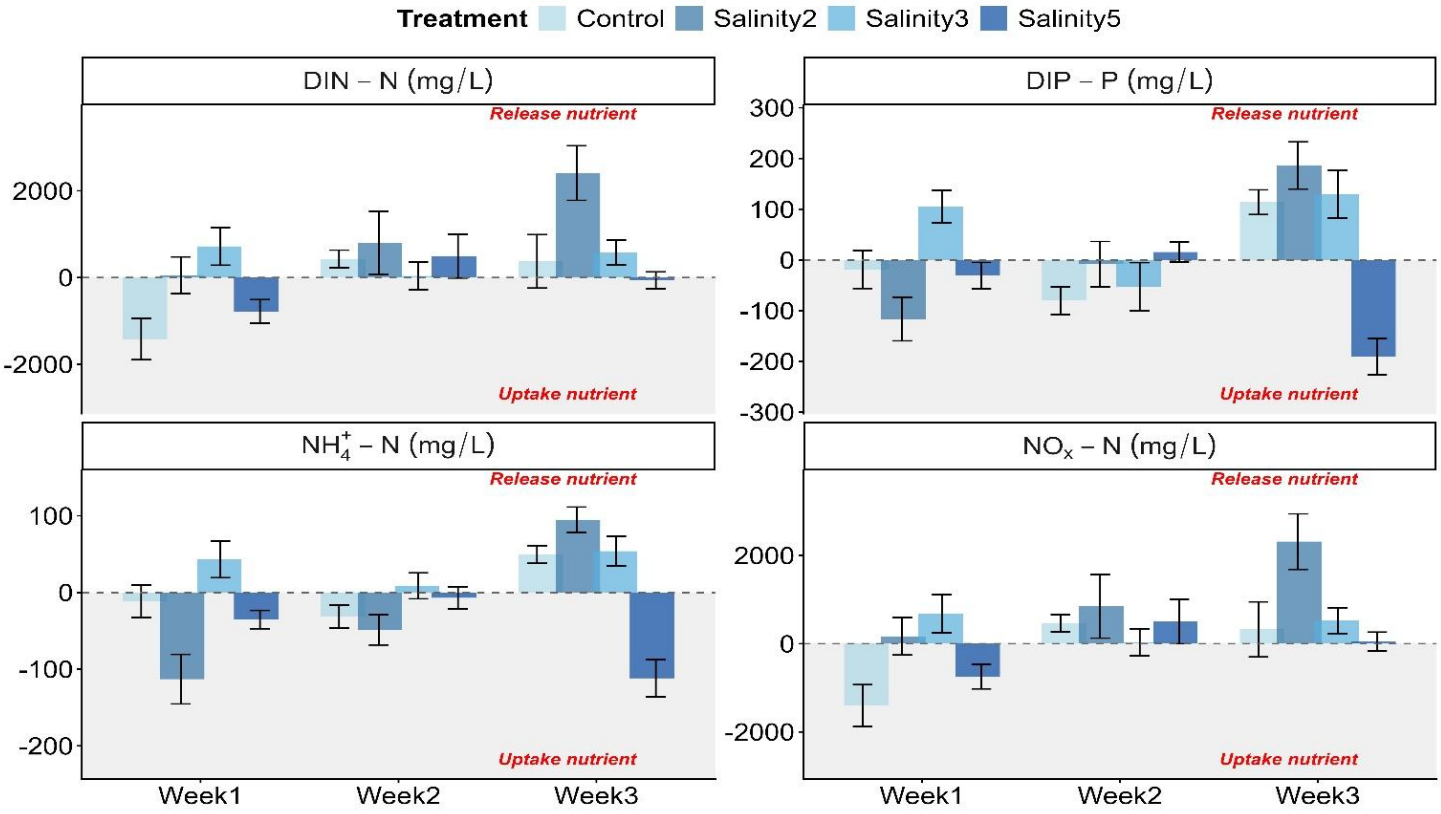

Fig. 7: Variation of nutrient concentrations in water showing patterns of release for DIN-N (dissolved inorganic Nitrogen), DIP-P (Dissolved inorganic phosphorus), $NH4^{+}$-N (Ammonium) and NO_x-N (Nitrite+Nitrate) in *Pontederia crassipes* exposed to increasing salinity in an ex-situ mesocosm experiment.

3.5 *Pontederia crassipes* decomposition in the continuum aquatic

The decomposition of 50g of *Pontederia crassipes* was monitored in environmental conditions ranging from freshwater to euhaline waters. At the freshwater, oligohaline and mesohaline–polyhaline sites, biomass loss became evident from day 7 onwards, indicating the onset of net decomposition. By contrast,

under euhaline conditions, biomass remained stable or increased slightly until day 15, after which decomposition became more pronounced (Fig. 8). Approximately 70% of the biomass decomposed throughout the experiment, with decomposition rates accelerating after day seven (Fig. 8, Table S13).

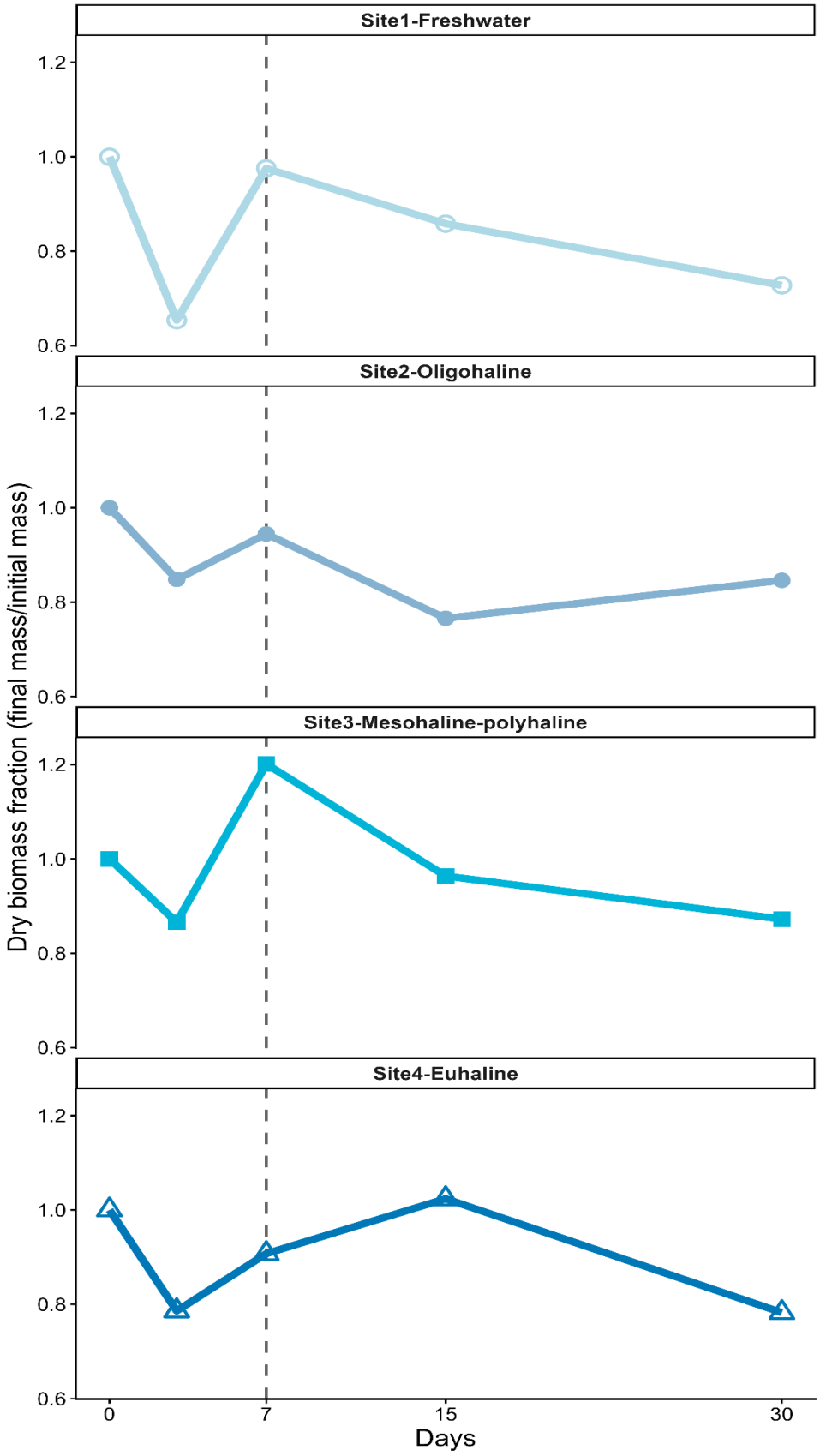

Fig. 8: The rate of decay of *Pontederia crassipes* in four three different types of aquatic environment: freshwater (Site1) oligohaline (Site 2), mesohaline-polyhaline waters (Site 3), and high euhaline waters (Site 4). The experiment was conducted over a period of 30 days.

Significant differences were observed between sites and over time for both dry remaining biomass (g) and the decay rate (k) after 30 days (Table 5). A significant interaction was detected for the decomposition rate (k), indicating that site-specific effects varied over time. Tukey's *post-hoc* test (Table S13) showed that on day 3, the freshwater site (Site1) exhibited a decay rate significantly higher than all other sites ($p<0.05$), a difference that dissipated by the day 7. Furthermore, the mesohaline-polyhaline site (Site 3) showed the most pronounced temporal variation, with a significant increase between the days 3 and 7, followed by a reduction. Regarding biomass fraction, Tukey's test confirmed the significant differences between day 3 and 7 ($p=0.0007$), 15($p = 0.0018$) and 30 ($p = 0.0315$), indication a rapid initial loss of *P. crassipes* in the first 15 days, followed by stabilization phase (Table S14).

Table 5: Results of two-way ANOVA testing the effects of measures of decomposition in *P. crassipes in-situ* experiment

	Time	Decomposition	Source of variation	Df	Sum of squares	Mean square	F statistic
30 Days							
	K	Site	3	0.009	0.003	4.019	0.016
		Time	3	0.055	0.018	25.538	< 0.001
		Site:Time	9	0.014	0.002	2.205	**0.049**
	Dry remain mass (g)						
		Site	3	0.173	0.058	4.603	**0.009**
		Time	3	0.357	0.119	9.496	**< 0.001**
		Site:Time	9	0.207	0.023	1.831	0.102
92 Days							
	K	Site	2	0.006	0.003	4.239	0.022
		Time	5	0.039	0.008	11.765	< 0.001
		Site:Time	10	0.021	0.002	3.209	**0.005**

Dry remain mass (g)	Site	2	0.097	0.048	2.467	0.099
	Time	5	0.915	0.183	9.335	< 0.001
	Site:Time	10	0.698	0.070	3.562	**0.002**

For the 92-day period, variation in both decay rate and dry biomass was observed over time across the three sites ($p < 0.002$; Table 5). Tukey's *post-hoc* tests (Table S16) confirmed that by day 92, the remaining dry biomass fraction was significantly lower at the mesohaline–polyhaline site (Site 3) compared to the freshwater (Site 1) and oligohaline (Site 2) sites (Fig. 9). Additionally, at the end of the 92-day period, Site 3 exhibited a significantly lower k value than Site 2 ($p < 0.001$) and a lower trend compared to Site 1 ($p = 0.095$; Table S15). This suggests that while *P. crassipes* decomposed more quickly in saline transition waters during the early stages, the process slowed down as recalcitrant material persisted. Overall, the plant lost 66% of its above-ground biomass under these conditions, with nutrient release patterns varying according to local salinity.

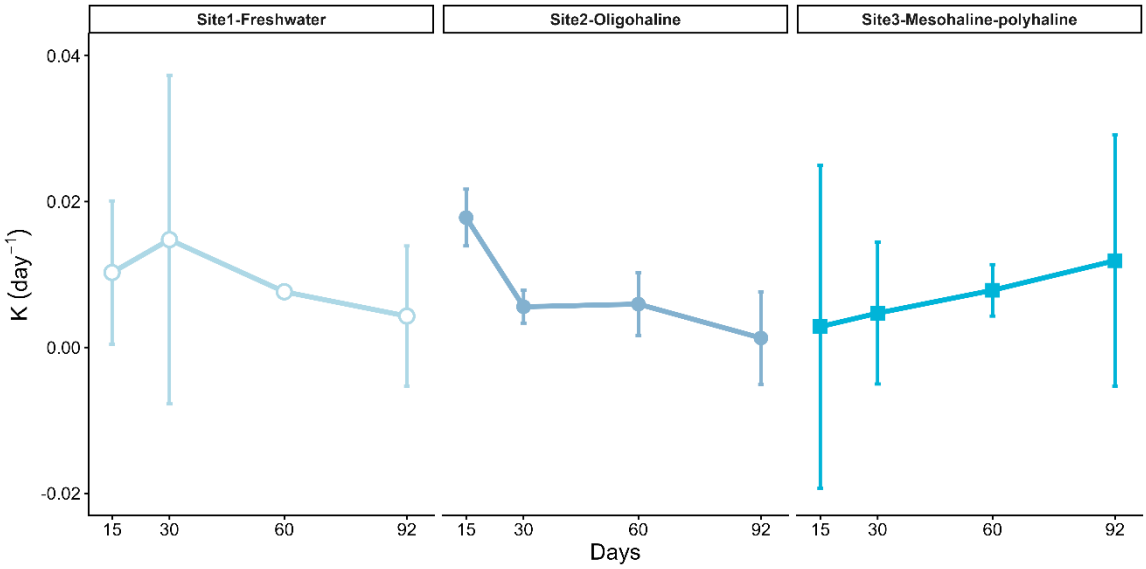

Fig. 9: Decay of *Pontederia crassipes* in three different types of water: oligohaline (Site 1 and Site 2), mesohaline/polyhaline water (Site 3). The experiment was conducted over a period of 92 days.

4.Discussion

4.1 Response of *Pontederia crassipes* to salinity gradient

Salinity exerted a strong control on the growth of *Pontederia crassipes*, with biomass reduction becoming evident within a few days at 5 g L^{-1}. This concentration falls within the hyposaline range (1–10 g L^{-1}), where non-halophytic macrophytes typically experience marked physiological stress (Moreira et al., 2023). The rapid decline observed here is consistent with reported tolerance thresholds for the species,

approaching critical limits near 6 g L^{-1} (Bick et al., 2020), indicating that oligohaline–mesohaline transitions represent a key ecological boundary for its performance.

The differential response among plant organs suggests that salinity tolerance is mediated by internal allocation strategies rather than uniform resistance. While older aerial tissues exhibited rapid senescence and chlorosis, roots and newly formed leaves remained comparatively stable. This pattern supports a stress-tolerance strategy based on the compartmentalization of toxic ions (Na^+ and Cl^-) in older tissues, allowing the maintenance of metabolic activity in younger structures (Moreira et al., 2023; Muramoto & Oki, 1988). Such selective allocation enables continued growth under suboptimal conditions, despite an overall decline in biomass accumulation.

The sustained production of new leaves even at 5 g L^{-1} further indicates that *P. crassipes* can maintain active physiological processes under moderate salinity stress. This behaviour is consistent with the tolerance range reported for widespread non-halophytes (Moreira et al., 2023) and suggests a capacity to persist in transitional environments. However, this resilience is accompanied by reduced growth efficiency, reflecting a shift from optimal performance towards survival-oriented functioning as stress increases.

Overall, these findings confirm that *P. crassipes* exhibits a threshold-dependent response to salinity, combining short-term tolerance with longer-term growth limitations. The use of a nutrient-balanced medium ensured that these responses were primarily driven by salinity stress rather than nutrient constraints, strengthening the interpretation of physiological limits under hyposaline conditions.

4.2 Modulation of water chemistry promoted by *Pontederia crassipes*

Our study found a significant interaction between time and salinity on pH and conductivity, supporting the existence of physiological feedback between *Pontederia crassipes* and its environment. The presence of plants resulted in notable acidification under control conditions (salinity <0.05 g L^{-1}). This active modulation is consistent with the findings of Song et al. (2024), who demonstrated that *P. crassipes* can significantly lower water pH (to values between 4.8 and 5.3) through the secretion of organic acids such as shikimic, stearic and palmitic acids. This biochemical interference alters the abiotic environment and as suggested by Song et al., may inhibit the growth of co-occurring species, thereby reinforcing the plant's invasive potential even under salinity stress.

The elevated electrical conductivity values recorded in this study reflect the combined effects of the imposed salinity treatments (2, 3, and 5 g L^{-1}) and the use of Hoagland nutrient solution as the experimental medium. Hoagland solution contains high concentrations of macro- and micronutrients in ionic form, and increasing its strength substantially alters the chemical composition and ionic load of the solution. Recent hydroponic studies have shown that different strengths of Hoagland solution significantly modify plant growth conditions by altering nutrient availability and ionic concentration (Majidi et al., 2025). Similarly, nutrient solutions supplemented with salts commonly reach high conductivity values while maintaining consistent treatment gradients (Ahmadi & Souri, 2020). In the present experiment, although absolute conductivity values exceeded those typically expected for oligohaline waters near the freshwater–brackish

transition, conductivity increased consistently with salinity across treatments. This confirms that the observed conductivity levels resulted from the nutrient-rich experimental medium combined with added salinity, while the intended exposure gradient was preserved.

Relative stability in dissolved oxygen (DO) and temperature indicates that the tested salinity gradient did not significantly impair oxygen solubility or accelerate microbial respiration to the point of hypoxia. The slight increase in DO observe during the second week coincided with a decrease in water temperature, consistent with the thermodynamic principles described by Debelius, Gómez-Parra and Forja (2009), who demonstrated that oxygen solubility in saline waters is primarily governed by an inverse relationship with temperature. These results therefore suggest that DO fluctuations were driven by seasonal cooling typical of late autumn conditions, rather than by biological oxygen demand associated with organic matter decay.

Expanding on current knowledge, this study addresses several key gaps. Although *P. crassipes* is widely recognized to cope with variations in pH (Song et al., 2024), conductivity (Churko et al., 2023) and temperature (Harun et al., 2021), salinity is often identified as a limiting factor (Moreira et al., 2023; Muramoto & Oki, 1988). Our findings confirm that, although productivity declines under oligohaline conditions, the species is able to maintain physiological functioning at concentrations of up to 5 g L^{-1}. This is consistent with reports of its occurrence in brackish habitats such as the Ria de Aveiro in Portugal (Laranjeira & Nadais, 2008) and Lake Nokoué in Nigeria (Sintondji et al., 2022), highlighting its capacity to persist across the aquatic continuum, including upstream estuarine zones.

Notably, our results reinforce the idea that *P. crassipes* does not merely respond to environmental conditions but actively modifies them, acting as a potential biogeochemical driver with significant long-term implications for coastal and inland ecosystems. During its active growth phase, the species promotes persistent acidification of the water column through the secretion of organic acids (Song et al., 2024). This capacity to alter the abiotic environment may create unfavorable conditions for salt-sensitive native species, thereby conferring a competitive advantage even under moderate salinity stress.

These findings are relevant for predicting future invasion dynamics under increasing freshwater salinization. Under altered hydrological conditions driven by sea-level rise, changes in precipitation patterns, or anthropogenic inputs such as industrial discharges and road salt runoff (Kelly et al., 2024), the demonstrated tolerance of P. crassipes to oligohaline conditions may enhance its competitive advantage over native aquatic species.

4.3 The source-sink transition: mechanisms of nutrient release and decomposition

Our findings confirm that *Pontederia crassipes* plays a significant role in shaping the dynamics of water quality in aquatic ecosystems. This free-floating macrophyte can absorb excess nutrients in its tissue, making it a promising candidate for phytoremediation under conditions involving petroleum residues and salinity (De Casabianca & Laugier, 1995). Its dense, fibrous root system and extensive surface area create an environment conducive to aerobic microorganisms utilising the organic matter and nutrients present in wastewater and converting them into organic compounds (Singh et al., 2023). Consequently, the roots can absorb dissolved nutrients directly from the water column (Rezania et al., 2015).

553 Overall, this study emphasises the potential of *P. crassipes* for phytoremediation in brackish
554 environments (1–3 g L^{-1}). However, the increase in nutrient concentrations beyond initial levels suggests that
555 nutrient dynamics were driven by the onset of decomposition following salinity exposure. Even in the control
556 group, a baseline release of nutrients was observed, likely representing the initial leaching of soluble
557 compounds from the standing biomass during the stabilization period in the mesocosms. This early-stage
558 leaching is a known physiological response during the transition of macrophytes to new environments.
559 Nevertheless, the effect of salinity remained clearly distinguishable, as higher salinity treatments significantly
560 accelerated tissue senescence and mass loss compared to the control, thereby intensifying the magnitude and
561 speed of nutrient release
562 Furthermore, our observed nutrient uptake patterns revealed that decomposing tissues released
563 nutrients back into the water. This indicates that while the species can effectively absorb nitrogen and
564 phosphorus at moderate salinity levels as also observed by Muramoto & Oki (1988) this capacity is transient.
565 These responses confirm that *P. crassipes* plays a dual role, acting as a nutrient sink during phytoremediation
566 and a nutrient source during decomposition. This transition exemplifies the assimilatory-dissimilatory
567 mechanism described by Gutiérrez et al. (2014), involving the cycling of energy and materials through the
568 uptake and subsequent release of nutrients.
569 Despite its beneficial attributes, *P. crassipes* is considered one of the most invasive aquatic plants
570 worldwide (IPBES, 2023). It can cause ecological impacts, such as oxygen depletion (Villamagna & Murphy,
571 2010) resulting from covering the surface of water, and economic impacts, such as the high costs of
572 mechanical control, as reported in Portugal (Laranjeira & Nadais, 2008). During warmer periods, particularly
573 in temperate regions, *P. crassipes* produce large amounts of biomass (Cavalli et al., 2015; Laranjeira &
574 Nadais 2008). Initially acting as a nutrient sink, this biomass later becomes a source of organic matter as it
575 decomposes in an assimilatory-dissimilatory process, influencing downstream ecosystems (Laranjeira &
576 Nadais 2008) in autumn and winter through changes in water chemistry and affecting parameters such as
577 conductivity, pH and nutrient availability (Song et al., 2024).
578 *Pontederia crassipes* can regulate nutrient dynamics by absorbing and releasing elements into the
579 water. The rate of decomposition is driven by leaching, which is most impacted by salinity, influencing the
580 release of nutrients, the accumulation of litter, and the quality of detritus (Balasubramanian et al., 2012;
581 Singhal et al., 1992). This study revealed that approximately 70% of a plant's biomass can decay in less than
582 92 days under continuous aquatic conditions. This suggests that biomass produced at the summer peak will
583 decompose and release nutrients during winter, particularly in connected systems such as estuaries and
584 coastal zones. Salinity was found to significantly affect the decomposition process, particularly during the
585 initial rapid leaching phase. This phase is characterised by the loss of ions and small organic compounds
586 within the first few hours or days (Singh et al., 2023). Although mesohaline–polyhaline conditions
587 accelerated the initial mass loss, the later stages associated with the decomposition of recalcitrant material
588 were delayed. This indicates a decoupling between the initial leaching phase and the long-term breakdown
589 of litter (Batistel et al., 2019).
590 Mesocosm experiments confirmed that *P. crassipes* releases significant quantities of nutrients in
591 saline conditions (1–5 g L^{-1}), which could affect the ecological integrity of transitional ecosystems and disrupt
592 nutrient cycling processes. In future climate scenarios, the intrusion of higher salinities is anticipated in the

upstream areas of estuaries and coastal waters (Buenos et al., 2025). This could enhance the ecological services provided by *P. crassipes*, which thrive in disturbed saline environments where decomposed biomass accumulates (Tootoonchi et al., 2023). Given its tolerance of a range of conditions and its rapid biomass production, this species could become more prevalent in such contexts. Its dual nature as both a risk and a resource poses a challenge for management, particularly in shallow, productive systems such as Pateira de Fermentelos lagoon where applying a single control method has proven ineffective over time.

Highlighting the challenge of managing this species, the dual nature of water hyacinth in terms of water quality is evident, as it can both clean and degrade water. This is emphasized by the Global Wetland Outlook 2025, which identifies invasive alien species as the primary cause of wetland loss and degradation. Therefore, integrated management strategies that control and manage the species throughout the aquatic continuum are essential. This is in line with Sustainable Development Goal 6 (Clean Water and Sanitation), which aims to protect and restore water-related ecosystems, such as wetlands.

5. Conclusion

According to this study, *Pontederia crassipes* can tolerate salinity levels ranging from <1 to 5 g L^{-1}, while maintaining its physiological functions and altering key water parameters such as pH and conductivity. While salinity restricts optimal growth and reproduction, this tolerance enables the species to persist in both freshwater and brackish environments, thereby expanding its ecological range and potential impact.

Salinity was found to significantly influence nutrient uptake and release, thus confirming the role of *P. crassipes* in nutrient dynamics, particularly under eutrophic or disturbed conditions. Mesocosm experiments revealed organ-specific growth responses and nutrient absorption under controlled gradients, and an *in-situ* study confirmed rapid nutrient release at higher salinities. Together, these results emphasise the species' competitive advantages as floating habit, rapid vegetative growth and high biomass production which reinforce its potential for phytoremediation and its threat to native communities.

The dual role of *P. crassipes* as both provider and a disruptor of ecosystem services emphasises the urgent need for an integrated management approach and highlights the pressing requirement for an integrated management approach. The results presented provide a vital foundation for developing predictive models that consider different environmental scenarios in coastal systems. Such models could inform more effective mitigation and conservation strategies, particularly in vulnerable estuarine environments. To mitigate the invasive potential of this species, particularly in vulnerable coastal areas, it is crucial to define adaptative limits and develop strategies.

628 **References**

629

630 Ahmadi, M., & Souri, M.K. (2020). Growth characteristics and fruit quality of chili pepper under higher
631 electrical conductivity of nutrient solution Induced by various salts. Agrivita Journal of Agricultural Science,
632 42(1), 143–152 http://doi.org/10.17503/agrivita.v42i1.2225

633

634 Almeida, D. P., Martins, D., Costa, N. V., Rodrigues, A. C. P., Pereira, F. A. R., & Cardoso, L. R. (2016).
635 Application volumes and sizes of droplets for the application of diquat herbicide in the control of *Eichhornia*
636 *crassipes*. *Planta Daninha, 34*(1), 145–154. https://doi.org/10.1590/S0100-83582016340100018

637

638 Azabo, M., Abdelhaleem, A., Fujii, M., & Nasr, M. (2024). *Pontederia crassipes* utilization for dual
639 phytoremediation and adsorption in greywater treatment: a techno-economic and sustainable
640 approach. *International Journal of Phytoremediation*, *26*(13), 2113–2126.
641 https://doi.org/10.1080/15226514.2024.2374887

642

643 Balasubramanian, D., Arunachalam, K., Das, A. K., & Arunachalam, A. (2012). Decomposition and nutrient
644 release of *Eichhornia crassipes* (Mart.) Solms. under different trophic conditions in wetlands of eastern
645 Himalayan foothills. *Ecological Engineering*, *44*, 111–122. https://doi.org/10.1016/j.ecoleng.2012.04.001

646

647 Bates D, Mächler M, Bolker B, Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4."*Journal*
648 *of Statistical Software*, 67(1), 1–48.doi:10.18637/jss.v067.i01.

649

650 Batistel, C. C., Jurasinski, G., & Schubert, H. (2019). Salinity exerted little effect on decomposition of
651 emergent macrophytes in coastal peatlands. *Science of the Total Environment, 658*, 126–136.
652 https://doi.org/10.1016/j.scitotenv.2018.12.011

653

654 Bellard, C., Marino, C. & Courchamp, F. (2022). Ranking threats to biodiversity and why it doesn't matter.
655 Nat Commun 13, 2616. https://doi.org/10.1038/s41467-022-30339-y

656

Bick, E., de Lange, E. S., Kron, C. R., da Silva Soler, L., Liu, J., & Nguyen, H. D. (2020). Effects of salinity and nutrients on water hyacinth and its biological control agent, *Neochetina bruchi*. *Hydrobiologia*, *847*, 3213–3224. https://doi.org/10.1007/s10750-020-04297-x

Borgwardt, F., Robinson, L., Trauner, D., Teixeira, H., Nogueira, A. J., Lillebø, A. I., ... & Culhane, F. (2019). Exploring variability in environmental impact risk from human activities across aquatic ecosystems. *Science of the total environment*, *652*, 1396-1408. https://doi.org/10.1016/j.scitotenv.2018.10.339

Brito, L. S., Thomaz, S. M., Teixeira, H., & Lillebø, A. I. (2026). Ex-situ growth protocol for the invasive macrophyte *Pontederia crassipes*. *MethodsX*, *16*, 103800. https://doi.org/10.1016/j.mex.2026.103800

Bueno, S.B., Pita-Barbosa, A., Roschildt, A.P., Castro, M.S., Borella, J. (2025) Hotspots, trends and future prospects of salinization: a scientometric analysis of the effects of salinization on aquatic plants. Hydrobiologia. https://doi.org/10.1007/s10750-025-05890-6

Cavalli, G., Baattrup-Pedersen, A., & Riis, T. (2015). Nutrient availability and nutrient use efficiency in plants growing in the transition zone between land and water. *Plant Biology, 18*(1), 90–97. https://doi.org/10.1111/plb.12397

Churko, E. E., Nhamo, L., & Chitakira, M. (2023). Phytoremediation Capacity of Water Hyacinth (*Eichhornia crassipes*) as a Nature-Based Solution for Contaminants and Physicochemical Characterization of Lake Water. *Water*, *15*(14), 2540. https://doi.org/10.3390/w15142540

Convention on Wetlands (2025) Global Wetland Outlook 2025: Valuing, conserving, restoring and f inancing wetlands. Gland, Switzerland: Secretariat of the Convention on Wetlands. DOI: 10.69556/GWO-2025-eng.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P., & van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. Nature, 387(6630), 253–260. https://doi.org/10.1038/387253a0

686 Custódio, M., Villasante, S., Calado, R., & Lillebø, A. I. (2021). Testing the hydroponic performance of the
687 edible halophyte *Halimione portulacoides*, a potential extractive species for coastal Integrated Multi-Trophic
688 Aquaculture. *Science of the Total Environment*, *766*, Artigo 144378. https://doi.org/
689 10.1016/j.scitotenv.2020.144378

690

691 De Casabianca, M.-L., & Laugier, T. (1995). *Eichhornia crassipes* production on petroliferous wastewaters:
692 Effects of salinity. *Bioresource Technology*, *54*(1), 39–43. https://doi.org/10.1016/0960-8524(95)00106-9

693

694 Debelius, B., Gómez-Parra, A. & Forja, J.M. Oxygen solubility in evaporated seawater as a function of
695 temperature and salinity. *Hydrobiologia* 632, 157–165 (2009). https://doi.org/10.1007/s10750-009-9835-4

696

697 Diagne, C., Leroy, B., Vaissière, A.-C., Gozlan, R. E., Roiz, D., Jarić, I., Salles, J.-M., Bradshaw, C. J. A.,
698 & Courchamp, F. (2021). High and rising economic costs of biological invasions worldwide. Nature, 592,
699 571–576. https://doi.org/10.1038/s41586-021-03405-6

700

701 Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Lévêque C, Sullivan CA et al (2006)
702 Freshwater biodiversity: importance, threats, status and conservation challenges. Biol Rev 81(2):163–182

703

704 Evangelista, H. B. A., Thomaz, S. M., & Umetsu, C. A. (2014). An analysis of publications on invasive
705 macrophytes in aquatic ecosystems. *Aquatic Invasions, 9*. https://doi.org/10.3391/ai.2014.9.3.01

706

707 Geletu, T. T. (2023). Lake eutrophication: Control of phytoplankton overgrowth and invasive aquatic weeds.
708 *Lakes & Reservoirs: Science, Policy and Management for Sustainable Use*, *28*(1), e12425.
709 https://doi.org/10.1111/lre.12425

710

711 Ghoussein, Y., Abou Hamdan, H., Fadel, A., Coudreuse, J., Nicolas, H., Faour, G., & Haury, J. (2023).
712 Biology and ecology of *Pontederia crassipes* in a Mediterranean river in Lebanon. *Aquatic Botany, 188,*
713 103681. https://doi.org/10.1016/j.aquabot.2023.103681

714

715 Gutiérrez, J. L., Jones, C. G., & Sousa, R. (2014). Toward an integrated ecosystem perspective of invasive
716 species impacts. *Acta Oecologica, 54*, 131–138. https://doi.org/10.1016/j.actao.2013.10.001

717

718 Harun, I., Pushiri, H., Amirul-Aiman, A. J., & Zulkeflee, Z. (2021). Invasive Water Hyacinth: Ecology,
719 Impacts and Prospects for the Rural Economy. Plants,10(8), 1613. https://doi.org/10.3390/plants10081613

720

721 Henares, M. N. P. & Camargo, A. F. M. Camargo. (2014). Estimating nitrogen and phosphorus saturation
722 point for Eichhornia crassipes (Mart.) Solms and Salvinia molesta Mitchell in mesocosms used to treating
723 aquaculture effluent. Acta Limnologica Brasiliensia, vol. 26, no. 4, p. 420-428.
724 http://dx.doi.org/10.1590/S2179-975X2014000400009

725

726 Hoagland, D. R., & Arnon, D. I. (1950). The water-culture method for growing plants without soil (Circular
727 No. 347). Berkeley, CA: University of California, College of Agriculture, Agricultural Experiment Station.

728

729 Hoffmann, W.A & Poorter, H. (2002). Avoiding bias in calculations of relative growth rate. Annals of
730 Botanica. 2002 Jul;90(1):37-42. doi: 10.1093/aob/mcf140.

731

732 IPBES (2023). Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species
733 and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystolon
734 Services. Roy, H. E., Pauchard, A., Stoett, P., Renard Truong, T., Bacher, S., Galil, B. S., Hulme, P. E., Ikeda,
735 T., Sankaran, K. V., McGeoch, M. A., Meyerson, L. A., Nuñez, M. A., Ordonez, A., Rahlao, S. J., Schwindt,
736 E., Seebens, H., Sheppard, A. W., and Vandvik, V. (eds.). IPBES secretariat, Bonn, Germany.
737 https://doi.org/10.5281/zenodo.7430692

738

739 Kelly, M., Teixeira, H., Lyche Solheim, A., Free, G., Phillips, G., Salas Herrero, M.F., Kolada, A., Varbiro,
740 G. and Poikane, S. (2024) Physico-chemical criteria to support Good Ecological Status in Europe,
741 Publications Office of the European Union, Luxembourg, doi:10.2760/355815, JRC136407.

742

743 Kobayashi, J. T., Thomaz, S. M., Pelicice, F. M. (2008). Phosphorus as a limiting factor for Eichhornia
744 crassipes growth in the Upper Paraná River floodplain. Wetlands, Volume 28, No. 4, pp. 905–91

745

746 Laranjeira, C. M., & Nadais, G. (2008). *Eichhornia crassipes control in the largest Portuguese natural*
747 *freshwater lagoon*. *Bulletin OEPP/EPPO Bulletin, 38*(3), 487–495. https://doi.org/10.1111/j.1365-
748 2338.2008.01268.x

749

750 Lenth, R. V. (2019). emmeans: Estimated marginal means, aka least-squares means (R package version
751 1.3.5). https://CRAN.R-project.org/package=emmeans

752

753 Lillebø, A. I., Teixeira, H., Morgado, M., Martínez-López, J., Marhubi, A., Delacámara, G., Strosser, P., &
754 Nogueira, A. J. A. (2019). Ecosystem-based management planning across aquatic realms at the Ria de Aveiro
755 Natura 2000 territory. *Science of The Total Environment, 650*(Part 2), 1898–1912.
756 https://doi.org/10.1016/j.scitotenv.2018.09.404

757

758 Luis, S., Pinho, M., Lopes, M. L., Oliveira, B. R. F., Sousa, A. I., & Lillebø, A. I. (2025). Are native species
759 of Ria de Aveiro under invasion? The relations between local activities and environmental perceptions on
760 marine biological resources. *Frontiers in Marine Science, 12*, Article 1603724.
761 https://doi.org/10.3389/fmars.2025.1603724

762

763 Majidi, A., Shahhoseini, R., Salehi-Arjmand, H. *et al.* (2025) Effect of Hoagland's nutrient solution strengths
764 and sodium silicate on growth, yield and biochemical parameters of Carla (*Momordica Charantia* L.) under
765 hydroponic conditions. *Sci Rep* 15, 7838 https://doi.org/10.1038/s41598-025-92616-2

766 Millennium Ecosystem Assessment. (2005). *Ecosystems and human well-being: Synthesis* (pp. 1–24). Island
767 Press.

768

769 Mittermeier, R. A., Turner, W. R., Larsen, F. W., Gascon, C.(2011). Global biodiversity conservation: The
770 critical role of hotspots. In *Biodiversity Hotspots* (pp. 3-22). Springer. https://doi.org/10.1007/978-3-642-
771 20992-5_1

772 Moreira, M. H., They, N. H., Rodrigues, L. R., Alvarenga-Lucius, L., & Pita-Barbosa, A. (2023). Salty
773 freshwater macrophytes: the effects of salinization in freshwaters upon non-halophyte aquatic plants.*The*
774 *Science of the total environment*, *857*(Pt 3), 159608. https://doi.org/10.1016/j.scitotenv.2022.159608

775

776 Muggeo, V. M. R. (2025). segmented: Regression models with break-points / change-points estimation (R
777 package version 2.1-4). Comprehensive R Archive Network (CRAN).
778 https://doi.org/10.32614/CRAN.package.segmented

779

780 Muramoto, S.; Aoyama. I; Oki, I.,. (1988). Effects of surface-active agents on the salinity tolerance of water
781 hyacinth (*Eichhornia crassipes*). *Journal of Environmental Science and Health, Part A: Environmental*
782 *Science and Engineering*, 23(6), 603–611. https://doi.org/10.1080/10934528809375437

783

784 Olson, J. S. (1963). Energy storage and the balance of producers and decomposers in ecological systems.
785 *Ecology, 44*(2), 322–331.

786

787 Pellegrini, M. O. de O., Horn, C., & Almeida, R. F. de. (2018). Total evidence phylogeny of Pontederiaceae
788 (Commelinales) sheds light on the necessity of its recircumscription and synopsis of Pontederia L. *PhytoKeys,*
789 *108*(1), 25–83. https://doi.org/10.3897/phytokeys.108.27652

790

791 Penfound, W. T., & Earle, T. T. (1948). The biology of the water hyacinth. *Ecological Monographs*, *18*(4),
792 447–472. https://doi.org/10.2307/1948585

793

794 Prasetyo, S., Anggoro, S., & Soeprobowati, T. R. (2021). Potential of water hyacinth (Eichhornia crassipes
795 (Mart.) Solms) in Rawapening lake as raw material for fish feed. Journal of Physics: Conference Series, 1943,
796 012072. https://doi.org/10.1088/1742-6596/1943/1/012072

797

798 Rezania, S., Ponraj, M., Talaiekhozani, A., Mohamad, S. E., Md Din, M. F., Mat Taib, S., Sabbagh, F., &
799 Md Sairan, F. (2015). *Perspectives of phytoremediation using water hyacinth for removal of heavy metals,*

organic and inorganic pollutants in wastewater. Journal of Environmental Management, 163, 125–133. https://doi.org/10.1016/j.jenvman.2015.08.018

Singh, C. K., Sodhi, K. K., & Singh, D. K. (2023). Understanding the bacterial community structure associated with the *Eichhornia crassipes* rootzone. *Molecular Biology Reports*, *51*(1), Artigo 35. https://doi.org/10.1007/s11033-023-08979-0

Singhal, P. K., Gaur, S., & Talegaonkar, L. (1992). Relative contribution of different decay processes to the decomposition of *Eichhornia crassipes* (Mart.) Solms. *Aquatic Botany*, *42*(3), 265–272. https://doi.org/10.1016/0304-3770(92)90027-G

Sintondji, S. W., Sohou, Z., Baetens, K., Lacroix, G., & Fiogbé, E. D. (2022). Characterization of a West African Coastal Lagoon System: Case of Lake Nokoué with Its Inlet (Cotonou, South Benin). *Ecologies* ,*3*(4), 467-479. https://doi.org/10.3390/ecologies3040033

Song U, Oh SH, Kim BW, Jeong S, Rim H (2024) *Pontederia crassipes* invasiveness on Jeju island is linked to a decline in water pH and climate change-driven overwintering. Aquatic Invasions 19(1): 35-49. https://doi.org/10.3391/ai.2024.19.1.117155

Tasker, S. J. L., Foggo, A., & Bilton, D. T. (2022). Quantifying the ecological impacts of alien aquatic macrophytes: A global meta-analysis of effects on fish, macroinvertebrate and macrophyte assemblages. Freshwater Biology, 67, 1847– 1860. https://doi.org/10.1111/fwb.13985

Téllez T. R., López E., Granado G., Pérez E., López R., Guzmán J. (2008). The Water Hyacinth, *Eichhornia crassipes*: an Invasive Plant in the Guadiana River Basin (Spain). Ai 3 (1), 42–53. 10.3391/ai.2008.3.1.8

Thomaz, S. M., & Cunha, E. R. (2010). The role of macrophytes in habitat structuring in aquatic ecosystems: Methods of measurement, causes and consequences on animal assemblages' composition and biodiversity. *Acta Limnologica Brasiliensia, 22*(2), 218–236. https://doi.org/10.4322/actalb.02202011

Thomaz, S. M. (2023). Ecosystem services provided by freshwater macrophytes. *Hydrobiologia, 850*, 2757–2777. https://doi.org/10.1007/s10750-021-04739-y

Tootoonchi, M., Gettys, L.A., Ferrell, J.A., Erickson, J.E., Bhadha, J.H.(2023) Salt tolerance assessment of aquatic and wetland plants: increased salinity can reshape aquatic vegetation communities. *Hydrobiologia* 850, 4575–4587. https://doi.org/10.1007/s10750-022-04934-5

Vaz, N., & Dias, J. M. (2011). *Caracterização sinóptica dos gradientes ambientais na Ria de Aveiro. Parte I: salinidade e temperatura*. In A. Almeida, F. L. Alves, C. Bernardes, J. M. Dias, N. C. M. Gomes, E. Pereira, H. Queiroga, J. Serôdio, & N. Vaz (Eds.), *Actas das Jornadas da Ria de Aveiro 2011* (pp. xx–xx). Universidade de Aveiro.

Villamagna, A. M., & Murphy, B. R. (2010). Ecological and socio-economic impacts of invasive water hyacinth (*Eichhornia crassipes*): A review. *Freshwater Biology*, *55*(2), 282–298. https://doi.org/10.1111/j.1365-2427.2009.02294.x

Wantzen, K. M., Ballouche, A., Longuet, I., Bao, I., Bocum, H., Cisse, L., Chuahan, M., Girard, P., Gopal, B., Kane, A., Marchese, M. R., Nautiyal, P., Teixeira, P., Zalewski, M., (2016). River Culture: an eco-social approach to mitigate the biological and cultural diversity crisis in riverscapes. Ecohydrology & Hydrobiology, volume 16, number 1, pages 7-18.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag. https://doi.org/10.18637/jss.v035.b01

Wilson, J.R., Holst, N., Rees, M., (2005) Determinants and patterns of population growth in water hyacinth. Aquatic Botany 81.51–67

Statements & Declarations

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Author contributions:

Ana Isabel Lillebø, Heliana Teixeira and Letícia da Silva Brito conceived the ideas and designed the methodology. Letícia da Silva Brito and Daniel Crespo collected the field data, and Letícia da Silva Brito and Heliana Teixeira analyzed it. Letícia da Silva Brito Heliana Teixeira and Ana Isabel Lillebø led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability statement: Supplementary Material 1 (Material Supplementary of the Statistical analyses).

Supplementary Files

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