

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

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Research Article

Keywords: Pontederia crassipes, mesocosm, decomposition, invasive alien species, ecosystem service, disservice

Posted Date: April 17th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-9227442/v1>

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1 **Title:** Salinity mediates ecosystem impacts of an invasive macrophyte across an aquatic continuum

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12
13 **Abstract:**

14
15 The ecological impacts of invasive species are increasingly recognized as context-dependent, yet
16 the role of environmental gradients in shaping these effects remains poorly understood. This is particularly
17 relevant in transitional aquatic ecosystems, where salinity gradients can constrain plant performance and alter
18 ecosystem functioning. We investigated how salinity influences the functional role of the invasive
19 macrophyte *Pontederia crassipes* by quantifying growth, nutrient uptake, and decomposition dynamics
20 across a freshwater–marine continuum. Using a combination of mesocosm experiments (0–5 g L⁻¹) and *in-*
21 *situ* litterbag assays along a natural salinity gradient (0–32 g L⁻¹), we assessed how key processes linked to
22 ecosystem functioning vary across environmental conditions. We found that plant growth and nutrient uptake
23 declined with increasing salinity, whereas decomposition rates increased markedly along with the gradient.
24 These contrasting responses indicate a shift in the functional role of the species, from nutrient retention in
25 freshwater systems to enhanced nutrient release under more saline conditions. Our results demonstrate that
26 environmental gradients strongly modulate the ecosystem impacts of invasive macrophytes, highlighting
27 salinity as a key driver of transitions between ecosystem service provision and ecosystem degradation. This
28 context dependency has important implications for predicting invasion impacts and for managing transitional
29 aquatic ecosystems.

30
31 **Keyword:** *Pontederia crassipes*; mesocosm; decomposition; invasive alien species; ecosystem service;
32 disservice.

33
34 **1 Introduction**

35 Freshwater ecosystems represent approximately 0.01% of the global water volume (Dudgeon et al.,
36 2006) and less than 1% of the global surface area (Mittermeier et al., 2011). Nevertheless, they play a

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

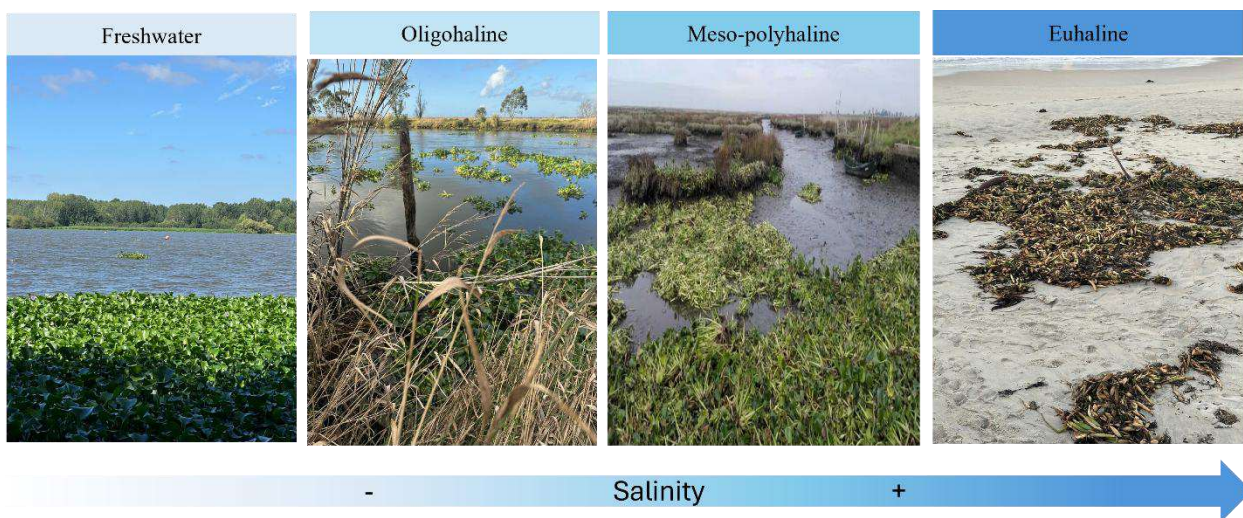
42 Despite their ecological importance, freshwater environments are under increasing threat from
43 multiple pressures (Borgwardt et al., 2019), such as biological invasions by alien species (Bellard et al.,
44 2022), including aquatic plants. Biological invasions are caused by organisms that are introduced, either
45 intentionally or unintentionally, in ecosystems outside of their native range. These organisms can then
46 establish and spread, causing ecological and economic harm (Tasker et al., 2022; Diagne et al., 2021).
47 According to the Wetland Global Assessment, invasions are the main cause of biodiversity loss in wetlands
48 (Convention on Wetlands, 2025). Besides biological invasions, freshwater systems suffer from
49 eutrophication symptoms, which are driven by excessive nutrient enrichment, particularly of nitrogen and
50 phosphorus (Geletu et al., 2023). Together, biological invasions and eutrophication can drastically alter the
51 structure and function of aquatic ecosystems. Macrophytes, with a central role in freshwater ecosystems by
52 contributing to primary production and habitat provisioning (Thomaz & Cunha, 2010; Evangelista et al.,
53 2014), can, conversely, generate ecosystem disservices, which refer to ecological processes or organisms that
54 result in negative consequences for ecosystems or human well-being. Relevant examples of disservices
55 include oxygen depletion, particularly at night when respiration is not compensated by photosynthesis,
56 increased biomass clogging waterways, and competitive exclusion of native flora (Villamagna & Murphy,
57 2010).

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

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

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

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



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

90

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

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

107

108 **2 Materials and Methods**

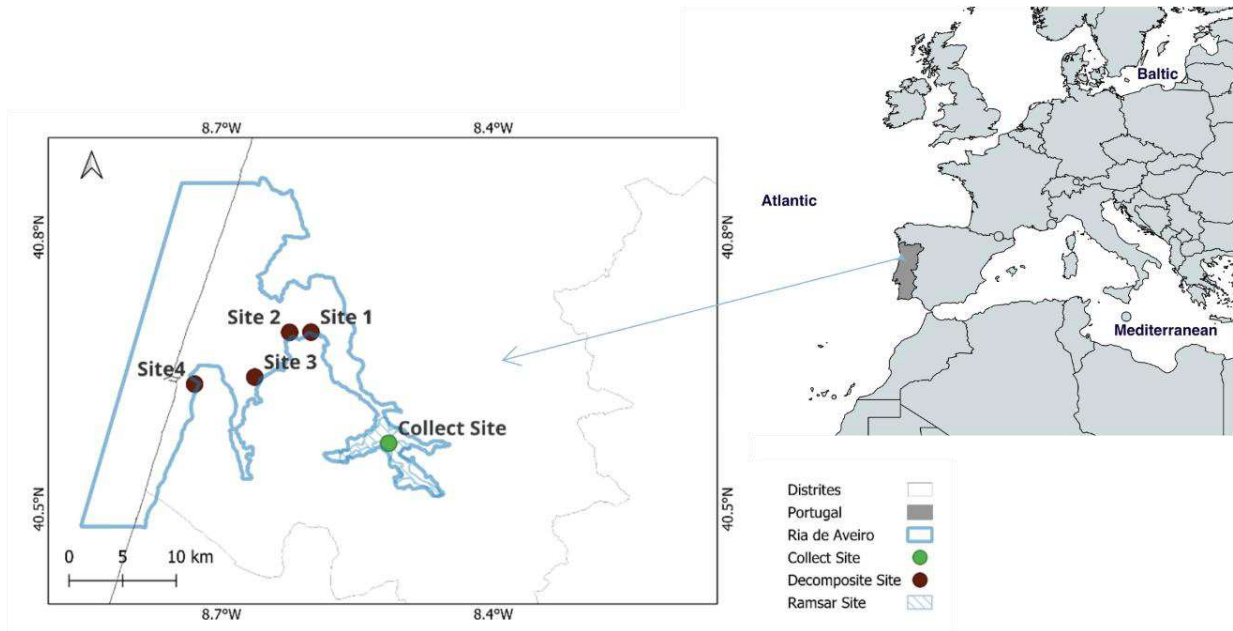
109

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

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

121 The *ex-situ* mesocosm experiments were conducted in a greenhouse facility at ECOMARE –
122 Laboratory for Innovation and Sustainability of Marine Biological Resources of the University of Aveiro.
123 The *in-situ* litter bag experiment took place in selected sites along the aquatic continuum (Fig. 2).
124 Experimental sites were chosen for their accessibility to minimise the risk of material loss during the
125 experiment. The oligohaline sites (Site 1: $40.6950702^\circ \text{N}$, 8.6249475°W ; Site 2: $40.6952281^\circ \text{N}$, 8.6013598°
126 W) had low salinity of 0.34 ± 0.63 and 1.3 ± 1.6 (mean \pm sd), respectively. In contrast, the
127 mesohaline/polyhaline and euhaline sites (Site 3: $40.6456448^\circ \text{N}$, 8.6634199°W ; Site 4: $40.6379169^\circ \text{N}$,
128 8.729826°W respectively) showed salinities of 24.5 ± 6.0 and 31.4 ± 1.9 (mean \pm sd) respectively, during
129 the experiments.

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



132

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

137

138 2.1 Mesocosm experiment

139 To verify the growth and nutrient uptake performance, we hypothesised that salinity along the
 140 freshwater–brackish water gradient significantly affects the growth and nutrient uptake of *P. crassipes*.
 141 Specifically, we tested the null hypothesis (H_0) that there are no significant differences in biomass growth
 142 and nutrient uptake rates across the aquatic continuum under mesocosm conditions. In the *ex-situ* experiment
 143 we used 20 plastic containers ($400 \times 300 \times 243$ mm; see Fig. 3), each containing 15 L of Hoagland solution
 144 and stocked with three healthy water hyacinths (average fresh biomass: 35.84 ± 12.81 g, mean \pm sd), sourced
 145 from the Pateira de Fermentelos lagoon, and maintained under natural light and temperature (20.0 ± 1.9
 146 °C, mean \pm sd). The study was conducted in a greenhouse for a period of four weeks. Prior to the start of
 147 the experiment, plants were acclimated for one week in Hoagland solution. After that, the salinity treatments
 148 simulating natural gradients from freshwater (<1 g L⁻¹) to transitional waters (2, 3, and 5 g L⁻¹), were
 149 introduced. A completely randomized design was applied to standardize conditions across all treatments.
 150 Each mesocosm trial lasted 28 days, with a water residence time approximately 10 days. Half of the nutrient
 151 solution was renewed weekly (Custódio et al., 2021).

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

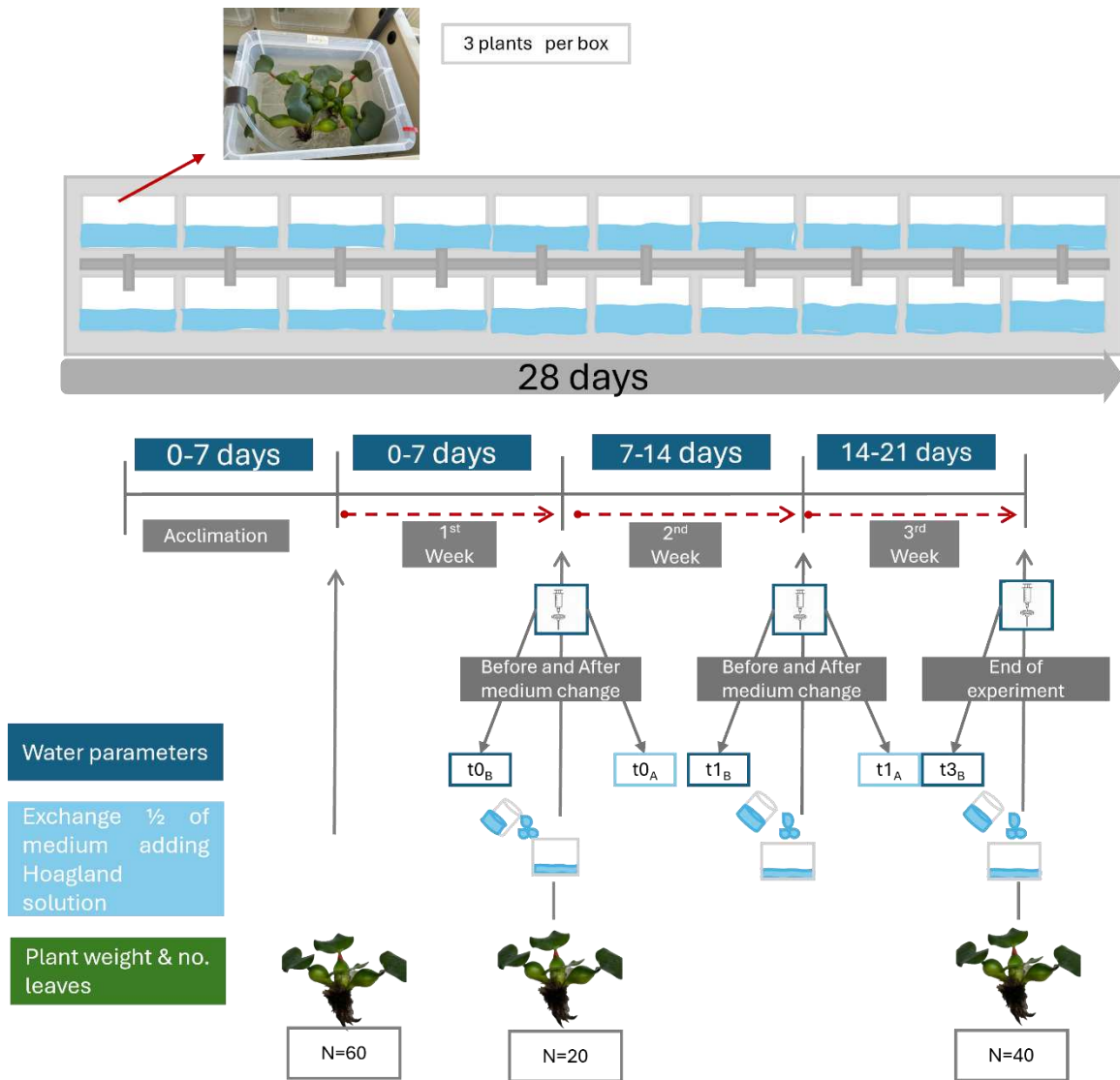
154 **Table 1:** Adapted Hoagland Solution nutrients components as described in Brito et al., 2026.

Hoagland's Stock Solutions (SS)	Stock Solution Concentration	Volume SS in Final Hoagland Solution
Macro nutrients SS		
1	1.00M NH ₄ H ₂ PO ₄	1ml/L
2	1.00M KNO ₃	6ml/L
3	1.00M Ca (NO ₃) ₂ 4H ₂ O	4ml/L
4	1.00M MgSO ₄ · 7H ₂ O	2ml/L
Micronutrient SS		
5	2.86g H ₃ BO ₃ /1L	1ml/L
	0.08 g CuSO ₄ ·5 H ₂ O /1L	
	0.22g ZnSO ₄ ·7H ₂ O /1L	
	1.81g MnCl ₂ /1L	
	0.02g H ₂ MoO ₄ /1L	
Iron stock		
6	26.1g EDTA /1L	0.25ml/L

155

156

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



162

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

165

166 2.1.1 Water analyses

167 Water samples (0.2 L) were filtered through 0.47 µm membranes (Custódio et al., 2021) before and
 168 after changing half of the volume of the solution in the boxes, every week (weeks 1, 2 and 3 of the experiment)
 169 (Fig. 3). The filtered samples were frozen at -20°C. pH was measured using a portable multiparameter meter
 170 (ProfiLine pH/Cond 3320, WTW, Germany), and dissolved oxygen was assessed with a portable oxygen
 171 meter (Oxi 3310, WTW, Germany). Concentrations of dissolved inorganic nutrients, namely ammonium
 172 (NH₄-N), nitrogen oxides (NO_x-N), and orthophosphate (PO₄-P), were determined using a Skalar San++
 173 continuous flow analyzer (Skalar Analytical, Netherlands). Dissolved inorganic nitrogen (DIN-N) was
 174 calculated as NH₄-N + NO_x-N, while dissolved inorganic phosphorus (DIP-P) was equal to PO₄-P.

175

176 2.1.2 Biomass measured

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

181

182 Total biomass

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

184 Liquid productivity

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

$$188 \text{ Liquid productivity} = (\text{Fresh weight final} - \text{Fresh weight initial} / \text{time}).$$

189 Productivity was expressed daily.

190 Relative Growth Rate

191 The Relative Growth Rate (RGR, day⁻¹) was calculated from the total dry mass (DM), of the plant
192 using the formula utilized by Hoffmann et al. (2002) (q. 2),

193

194 (Equation 2)

$$195 \text{ RGR} = (\ln M_n - \ln M_{n-1}) * t^{-1}$$

196 where:

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

200

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

206

207 2.2 Decomposition experiment

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

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

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

222

223 (Equation 3)

224

225

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

226

227 where:

228

- 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.

229

230

231

232

233

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

241

242

243

244

(Equation 4)

245

246

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

247

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

256 2.3 Statistical analyses

257
258
259 For the *ex-situ* mesocosm experiments, we statistically analysed water parameters oxygen content,
260 temperature, conductivity and pH. For each parameter, measured in twelve independent groups, each with
261 five replicates ($n = 5$), the group means and standard deviations were calculated, and an overall mean was
262 obtained by averaging group means; variability was estimated using a pooled standard deviation (sd) of the
263 standard deviations in each group, from which the standard error of the mean (SEM) and 95% confidence
264 interval (CI) were derived assuming a t-distribution ($df=59$, 5 reps*12 groups).

265 To assess the effect of treatment over time, each of the above water parameters, plant and nutrients
266 (DIN-N, DIP-P, $\text{NH}_4^+\text{-N}$ and $\text{NO}_x\text{-N}$) were analysed using a linear mixed-effects model fitted with the *lmer()*
267 function from the *lme4* package (Bates et al., 2015). Treatment, Week and their interaction were included as
268 fixed effects. To control for pseudo replication, Box was included as a random effect. Repeated measures
269 analysis of variance (ANOVA) was used to test for significant effects, followed by a Tukey's post hoc test
270 using the *emmeans* package (Lenth, 2019). For RGR, as the variance among boxes was negligible and the
271 mixed-effects model failed to converge, a two-way ANOVA was fitted using a standard linear model *lm()*,
272 with treatment, week, and their interaction as fixed factors.

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

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

279 **3. Results**

280 **3.1 Physico-chemical variations in water under *Pontederia crassipes* exposure to a salinity gradient**

281
282
283 During the 28 days experiment, oxygen concentrations remained rather stable (Table 2), despite
284 week 2 showing significantly higher mean values (9.98 mg/L) than the first and last weeks of the experiment
285 (Fig. S1, Table S2). Nonetheless, observed values during the entire experiment were within adequate levels
286 to support good ecological aquatic functions, with a (relatively small overall standard error (SEM = 0.08, n

287 = 60; Table S1) across all settings and mean oxygen concentrations laying between a narrow 95% confidence
 288 interval (CI) of 9.56 to 9.88 mg/L. Likewise, in week 2 water temperature significantly differed from the
 289 other periods, showing a slight decreased in mean values (14.6 °C) (Fig. S2, Table S3). Nonetheless,
 290 temperature variation across settings was small (SEM=0.28; Table S1) and within expected ranges (Table 2)
 291 for the late autumn season in the system (95% CI from 15.45 to 16.56 °C; Table S1), indicating stable and
 292 well-controlled experiment conditions.

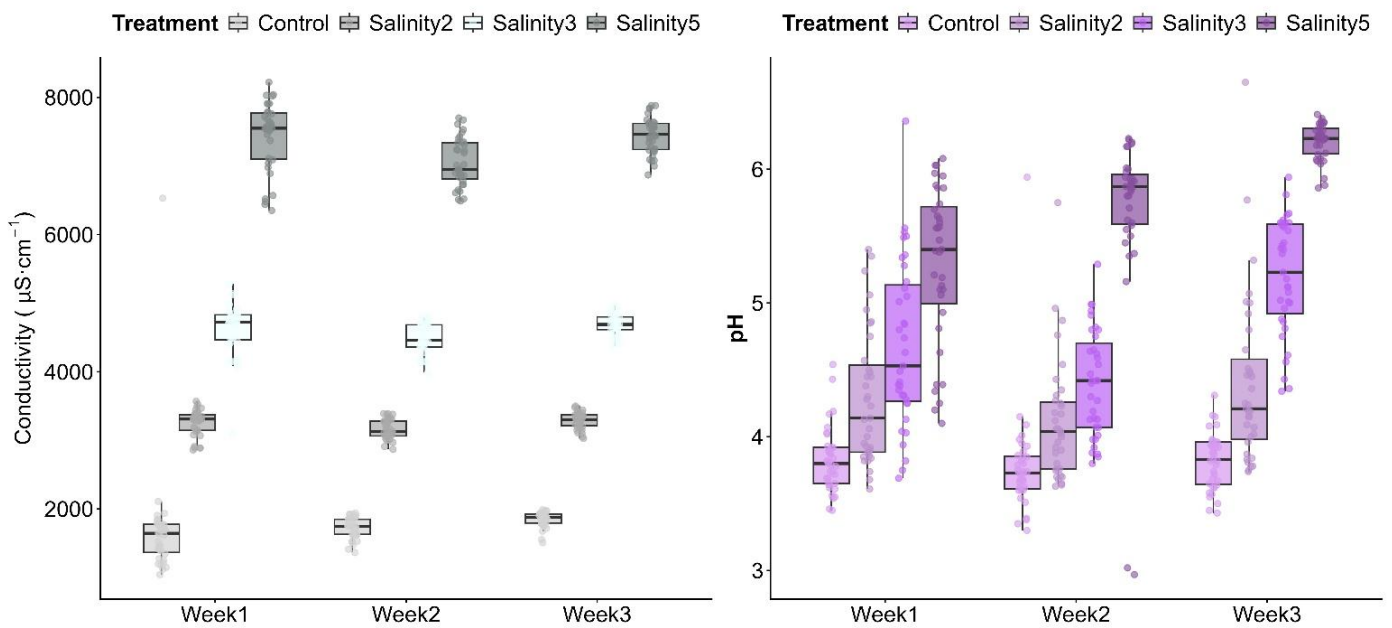
293 **Table 2:** Water parameters variation (mean ± sd) in *P. crassipes* whole plant mesocosm *ex-situ* experiment
 294 over a 3-Week period under different salinity exposure conditions (Treatment). † post-hoc Tuckey Test
 295 significantly different groups ($p < 0.001$)

	Treatment	Oxygen (mg/L)	Temperature (°C)	Conductivity (µs/cm)	pH
<i>Week1</i>	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
<i>Week2</i>	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
<i>Week3</i>	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					
<i>Treatment effect</i>	F (df=3)	0.22 (p=0.88)	0.68 (p=0.578)	2035.70 (p<0.001)	42.65 (p<0.001)
<i>Week effect</i>	F (df=2)	27.60 (p<0.001)	40.65 (p<0.001)	13.21 (p<0.001)	43.91 (p<0.001)
<i>Treatment:Week</i>	F (df=6)	0.09 (p=0.99)	0.019 (p=1.0)	2.68 (p=0.03)	12.684 (p<0.001)

296 Conductivity and pH conditions differed significantly across salinity exposure conditions during the
 297 entire duration of the experiment, with increasing values observed at increasingly salinity conditions (Table
 298 2 and Fig. 4). The salinity exposure treatment effect in conductivity was expected, and control conditions
 299 presented the lower mean conductivity values of 1757 µS/cm (Table 2), which in this experiment were higher
 300 than the normal range expected for freshwater conditions. The mean conductivity values for the exposure
 301 treatments across oligohaline conditions (2, 3 and 5 g L⁻¹) were respectively 3236, 4603 and 7311 µS/cm
 302 (Fig. 4), which were also higher than expected for brackish waters near the freshwater spectrum. During the
 303 experiment, conductivity conditions remained quite stable across all treatments, expect for week 2 in the
 304 higher exposure treatment (Table S4) where it showed a significant dip with respect to the values observed

305 in the previous and subsequent week (Fig. 4), but still with values above 7000 $\mu\text{S}/\text{cm}$ (Table 2), higher than
306 the other treatments.

307 For pH, during the entire duration of the experiment, a lower acidity pattern was generally observed
308 with increasing salinity exposure, despite some overlap between treatment 2 and 3 during the first two weeks
309 (Table S5), but still the mean pH was higher at the higher exposure (Table 2). Unlike the other water
310 parameters, for pH at the higher salinity exposure treatments (3 and 5 g L^{-1}) there was a significant
311 difference between the starting conditions (at week 1) and the end of the experiment (in week 3), where pH
312 values registered significant increases (Table 2). This increase was observed already in the second week for
313 the highest exposure (Table S5; Fig. 4), and kept increasing significantly, until the end of the experiment; up
314 to 5.20 ± 0.43 in exposure 3 g L^{-1} and in the highest exposure up to just slightly acidic conditions ($6.21 \pm$
315 0.14), reaching the lower limit of the tolerable range for most aquatic life. In the control and in the lowest
316 exposure treatment (2 g L^{-1}) no relevant pattern was observed (Table S5) and mean water conditions remained
317 highly acidic across the entire experiment (mean treatment values around 3.8 and 4.3 respectively).



318

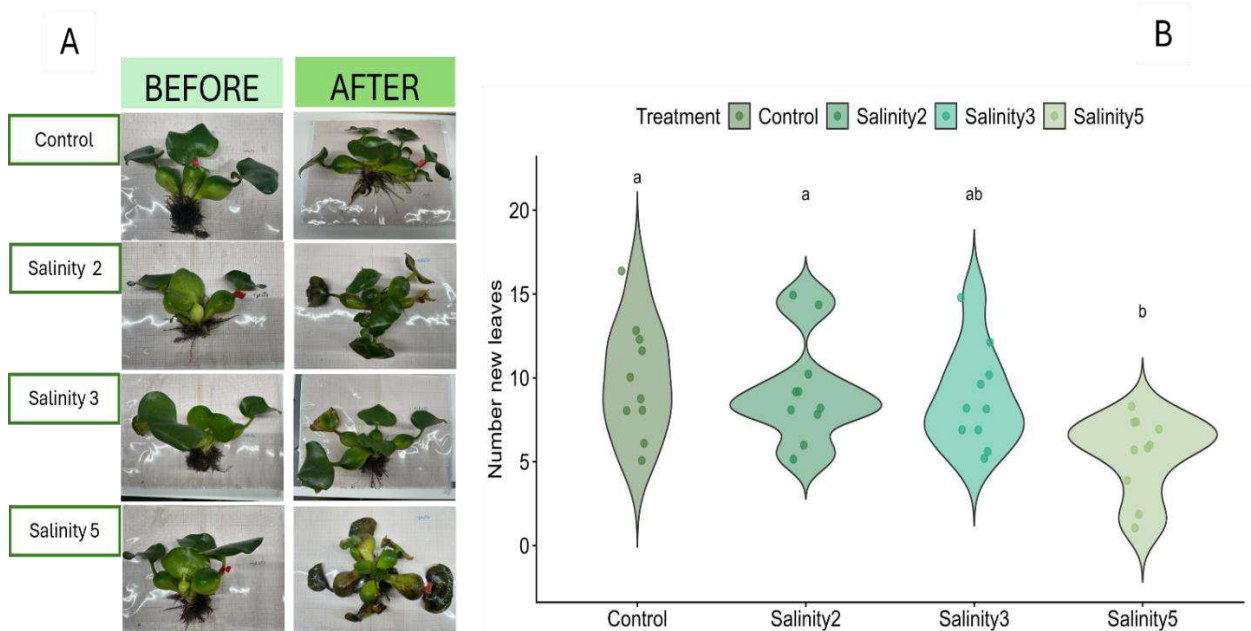
319 **Fig. 4:** Variation of conductivity and pH in *Pontederia crassipes* under salinity mesocosm experiment over
320 the weeks.

321

322 3.2 Impact of salinity gradient on *Pontederia crassipes* leaf growth

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

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



330
 331 **Fig. 5:** (A) Visual representation of *Pontederia crassipes* before and after exposure to salinity treatments in
 332 the *ex-situ* mesocosm experiment. The images illustrate plant structure prior to treatment and at the end of
 333 the experimental period; (B) The number of leaves produced under different levels of salinity exposure.
 334 Letters indicate statistically significant differences across treatments.

335
 336 Although, in this experiment, leaf emergence suggests slight tolerance of *P. crassipes* to salinity
 337 increase, plants at the highest salinity concentration (5 g L⁻¹) exhibited chlorosis within a few days (author
 338 personal observation during the course of the experiment; similarly to chlorosis observed in Fig. 5A photo
 339 taken at the end of the experiment from the two highest exposure treatments).

340
 341 **3.3 Potential growth of *Pontederia crassipes* along the aquatic continuum**

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

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

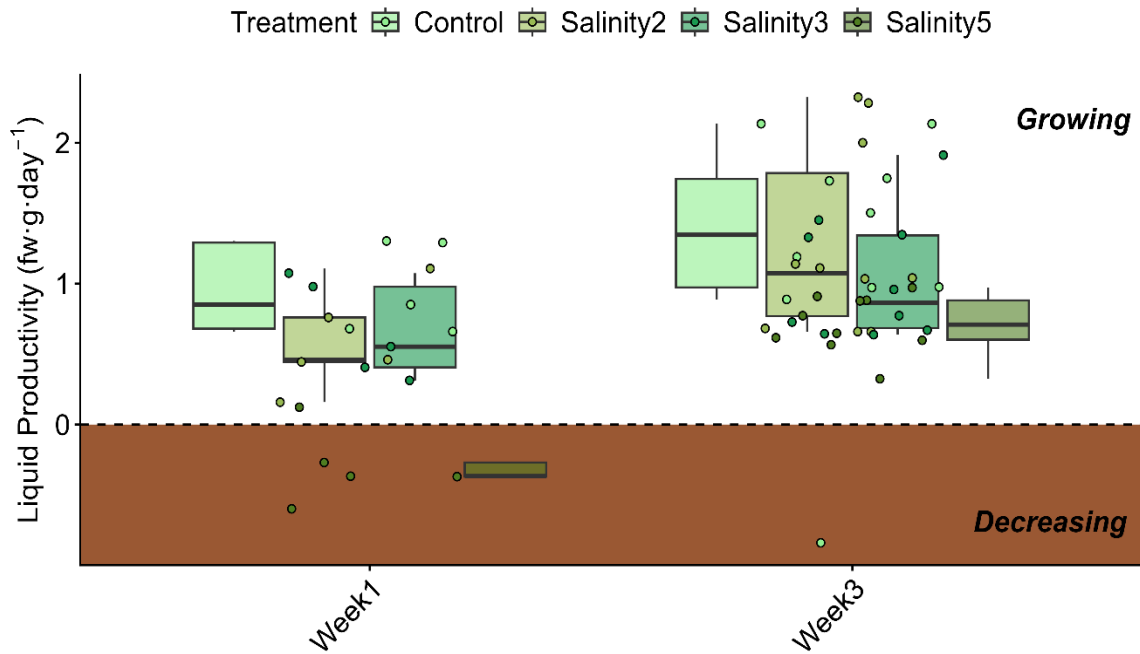
348 of days, which presented positive values in most settings, indicating favourable growth conditions overall
 349 (Table 3), expect for the highest exposure treatment where a decrease was observed during the first week
 350 (Fig. 6). In fact, the liquid productivity shows a significant increase for 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)

357



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

361

362 **3.4 Impact of salinity on nutrient uptake by *Pontederia crassipes***

363

364 Release or uptake of nutrients in water by *P. crassipes* varied markedly across salinity treatments
 365 and such patterns changed throughout the duration of the experiment (Fig. 7). The negative value represents
 366 the uptake of nutrients from water by plants. All nutrient concentration dynamics (DIN-N, DIP-P, NH₄⁺-N
 367 and NO_x-N) were significantly affected by salinity and exposure time (Table 4; Supplementary Material Table
 368 S19-S12). Nonetheless the highest uptake or release concentrations were generally observed under higher
 369 and longer exposures (Fig. 7).

370

371 Table 4: Nutrients concentrations in water (mean ± sd) in *Pontederia crassipes* mesocosm experiment over
 372 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)
<i>Initial concentrations at t0:</i>		224.60 ± 66.62	26.80 ± 6.57	9.02 ± 4.08	215.58 ± 66.01
Treatment	Week				
<u>Control</u>	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

<u>Salinity2</u>	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
<u>Salinity3</u>	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
<u>Salinity5</u>	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

<i>Treatment</i>	F(df=3)	5.13 (p=0.003)	6.30 (p=0.001)	10.40 (p<0.001)	5.09 (p=0.004)
<i>Time</i>	F (df=2)	6.95 (p=0.002)	6.82 (p=0.002)	7.48 (p=0.001)	6.45 (p=0.003)
<i>Treatment: Time</i>	F (df=6)	2.63 (p=0.028)	10.93 (p<0.001)	11.72 (p<0.001)	2.34 (p=0.046)

373

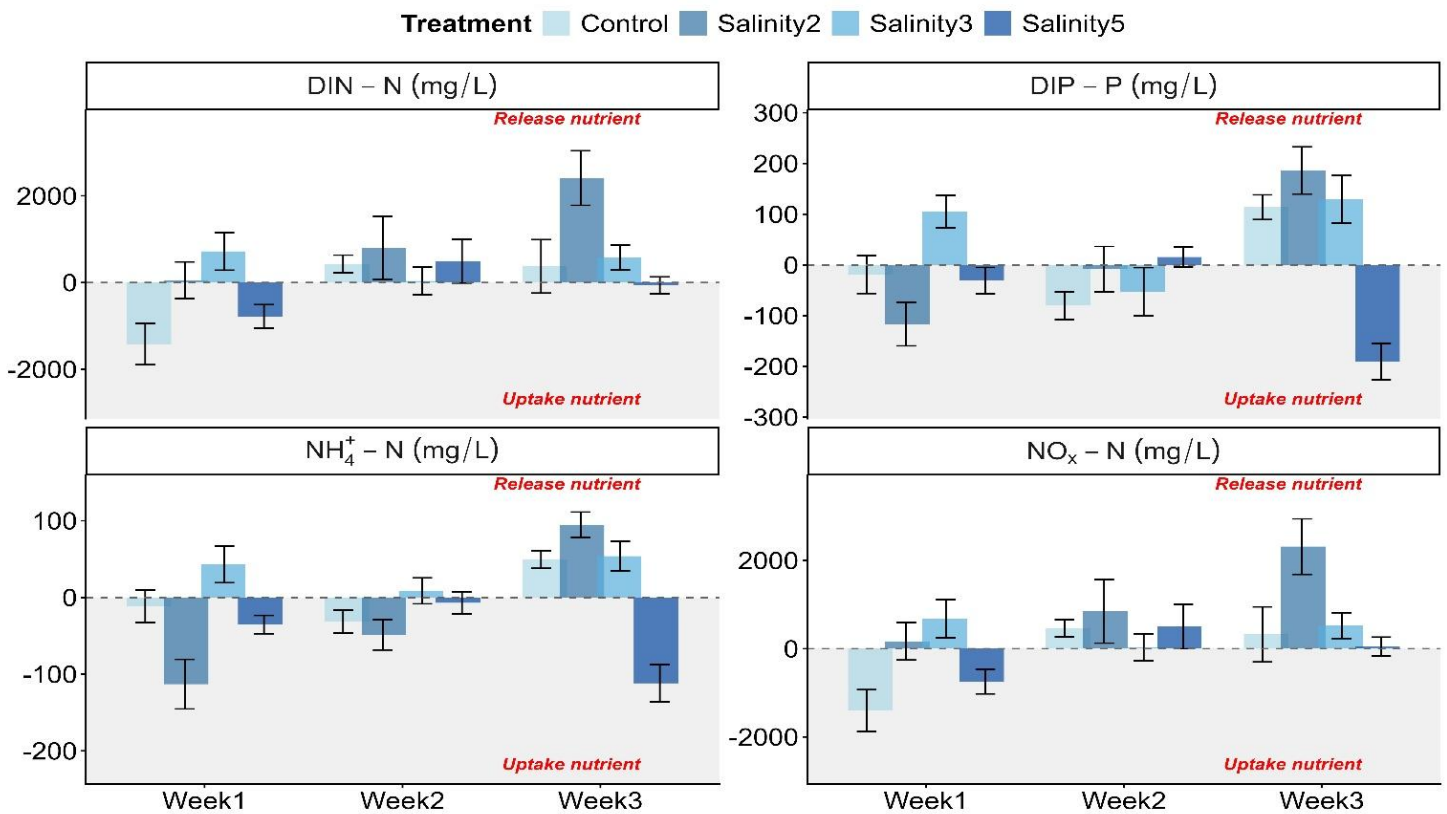
374 For Phosphorus, early in the experiment, conditions under control and low salinity exposure (2 g
375 L⁻¹), there is a higher uptake or a net balance between release and uptake that changes significantly into a
376 clear release pattern towards the end of the experiment (Fig 7; Table S9). At intermediate exposure (3 g
377 L⁻¹) there is initially a DIP-P release pattern followed by an uptake and then again, a significant shift
378 towards a release of Phosphorus. At the highest exposure, initial uptake is followed by a balance between
379 release and uptake and then a significant change towards strong release of Phosphorus into water by the
380 end of the experiment (Fig. 7; Table S9). For Ammonium, very similar patterns to those of Phosphorus
381 were observed (Fig. 7), although trends were not always as expressive thus not all variations are
382 significantly different (Table S10). Under control conditions and low salinity exposure (2 g L⁻¹) there is a
383 shift from uptake to release towards the end of the experiment (Fig. 7; Table S10). At intermediate exposure
384 (3 g L⁻¹) there is mostly an Ammonium release pattern trend. On the contrary, at the highest exposure,
385 Ammonium uptake by the plant seems to dominate early on and significantly increase by the end of the
386 experiment (Fig. 7; Table S10).

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

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

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

406



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

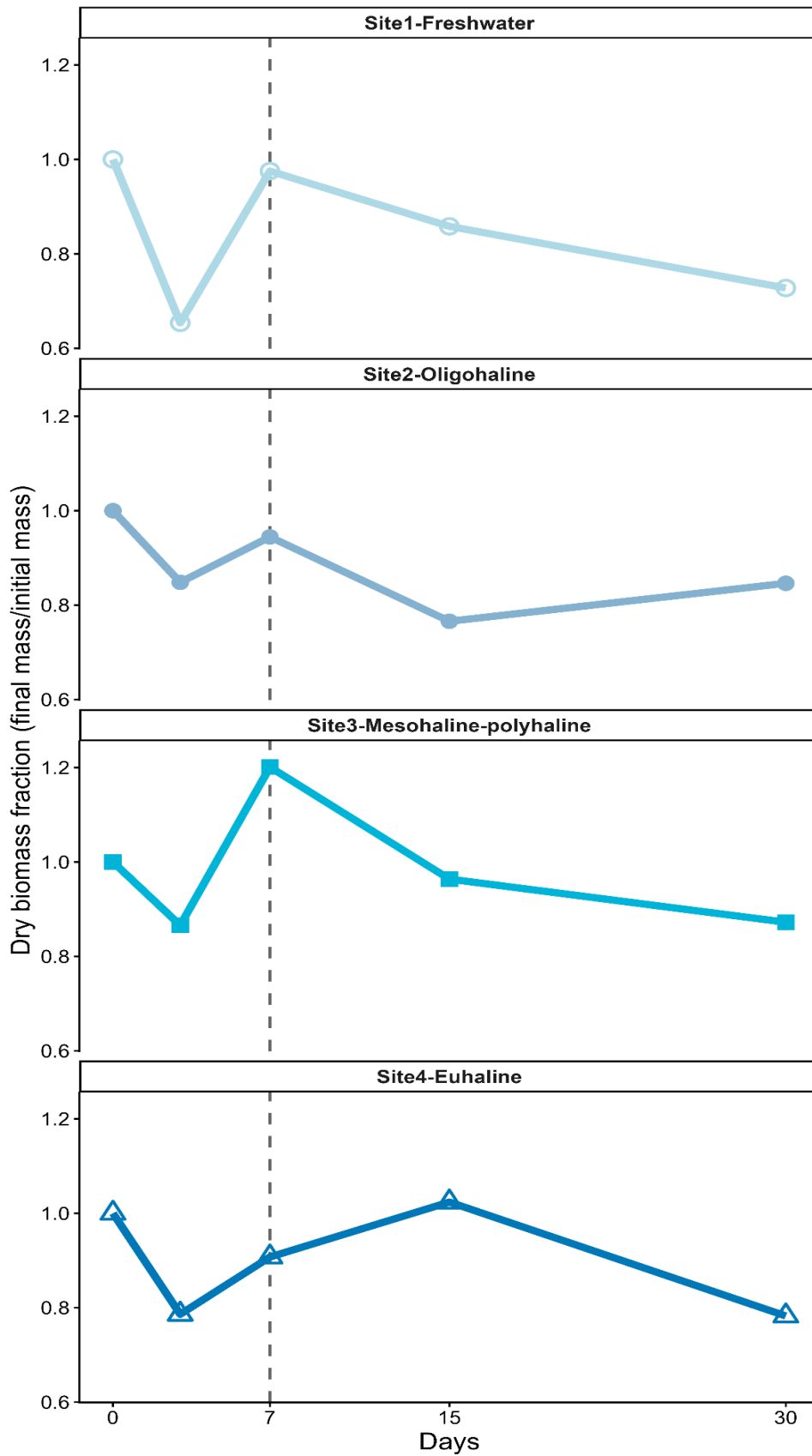
410

411 3.5 *Pontederia crassipes* decomposition in the continuum aquatic

412

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

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



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

442

443 Significant differences were observed between sites and over time for both dry remaining biomass
 444 (g) and the decay rate (k) after 30 days (Table 5). A significant interaction was detected for the decomposition
 445 rate (k), indicating that site-specific effects varied over time. Tukey's *post-hoc* test (Table S13) showed that
 446 on day 3, the freshwater site (Site1) exhibited a decay rate significantly higher than all other sites ($p < 0.05$),
 447 a difference that dissipated by the day 7. Furthermore, the mesohaline-polyhaline site (Site 3) showed the
 448 most pronounced temporal variation, with a significant increase between the days 3 and 7, followed by a
 449 reduction. Regarding biomass fraction, Tukey's test confirmed the significant differences between day 3 and
 450 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
 451 days, followed by stabilization phase (Table S14).

452

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

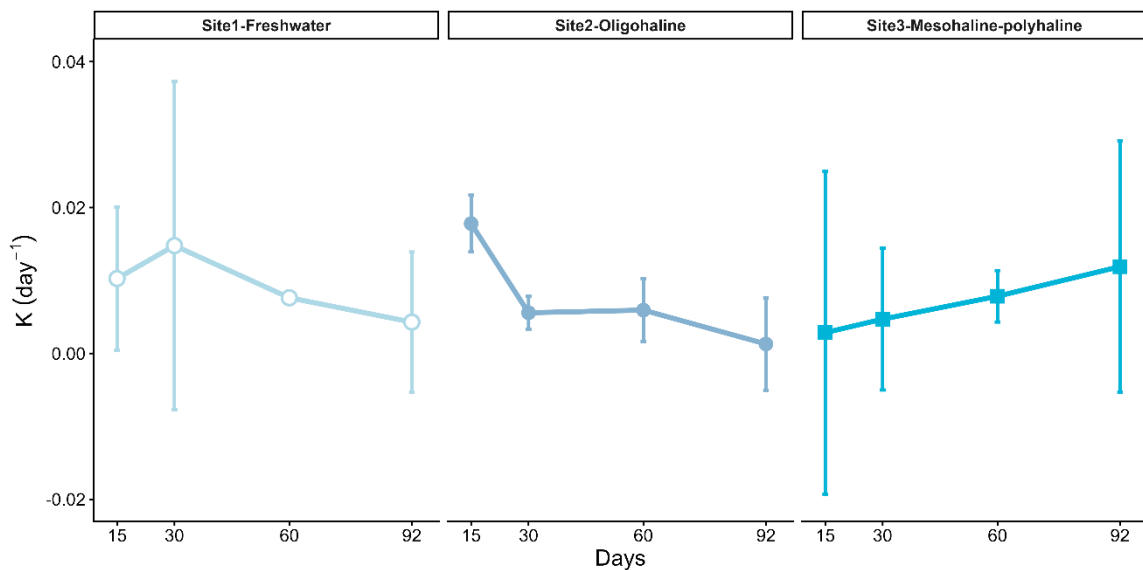
455

Time	Decomposition	Source of variation	Df	Sum of squares	Mean square	F statistic
30 Days						
<i>K</i>	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
<i>Dry remain mass (g)</i>						
	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						
<i>K</i>	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

456

457 For the 92-day period, variation in both decay rate and dry biomass was observed over time across
 458 the three sites ($p < 0.002$; Table 5). Tukey's *post-hoc* tests (Table S16) confirmed that by day 92, the
 459 remaining dry biomass fraction was significantly lower at the mesohaline–polyhaline site (Site 3) compared
 460 to the freshwater (Site 1) and oligohaline (Site 2) sites (Fig. 9). Additionally, at the end of the 92-day period,
 461 Site 3 exhibited a significantly lower k value than Site 2 ($p < 0.001$) and a lower trend compared to Site 1 (p
 462 = 0.095; Table S15). This suggests that while *P. crassipes* decomposed more quickly in saline transition
 463 waters during the early stages, the process slowed down as recalcitrant material persisted. Overall, the plant
 464 lost 66% of its above-ground biomass under these conditions, with nutrient release patterns varying according
 465 to local salinity.



466

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

469 **4. Discussion**

470

471 **4.1 Response of *Pontederia crassipes* to salinity gradient**

472

473 Salinity exerted a strong control on the growth of *Pontederia crassipes*, with biomass reduction
 474 becoming evident within a few days at 5 g L⁻¹. This concentration falls within the hyposaline range (1–10 g
 475 L⁻¹), where non-halophytic macrophytes typically experience marked physiological stress (Moreira et al.,
 476 2023). The rapid decline observed here is consistent with reported tolerance thresholds for the species,

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

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

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

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

495

496 **4.2 Modulation of water chemistry promoted by *Pontederia crassipes***

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

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

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

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

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

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

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

543

544 **4.3 The source-sink transition: mechanisms of nutrient release and decomposition**

545

546 Our findings confirm that *Pontederia crassipes* plays a significant role in shaping the dynamics of
547 water quality in aquatic ecosystems. This free-floating macrophyte can absorb excess nutrients in its tissue,
548 making it a promising candidate for phytoremediation under conditions involving petroleum residues and
549 salinity (De Casabianca & Laugier, 1995). Its dense, fibrous root system and extensive surface area create an
550 environment conducive to aerobic microorganisms utilising the organic matter and nutrients present in
551 wastewater and converting them into organic compounds (Singh et al., 2023). Consequently, the roots can
552 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

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

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

605

606 **5. Conclusion**

607

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

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

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

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855 **Statements & Declarations**

856 **Funding**

857 This worked was supported by national resources through the FCT – Fundation for Science and
858 Tecnologia I.P, in the projects CESAM-Centre of Studies and Environmental and Sea, references
859 UID/50017/2025 (doi.org/10.54499/UID/50017/2025) and LA/P/0094/2020
860 (doi.org/10.54499/LA/P/0094/2020). Leticia da Silva Brito was funded by FCT under the PhD Grant
861 2021.07101.BD. Heliana Teixeira was funded by FCT under the project CEECIND/08095/2022. This study
862 was funded by the project RESTORE4Cs (DOI: 10.3030/101056782), funded by the European Union under
863 the Horizon Europe research and innovation programme (Grant Agreement ID: 101056782) in close
864 collaboration with the ERA Chair BESIDE (DOI: 10.3030/951389) financed by the European Union’s
865 Horizon 2020 research and innovation programme (Grant agreement ID: 951389).

866 **Competing Interests**

867 The authors have no relevant financial or non-financial interests to disclose.

868 **Author contributions:**

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

874

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

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