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RESEARCH

Influence of reproductive cell density of *Ulva ohnoi* (Ulvophyceae) in seeded Algal Turf Scrubbers (sATS): biomass yield and bioremediation implications

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Abstract

The genus *Ulva* has gained prominence in aquaculture due to its rapid growth, adaptability, and capacity to deliver ecosystem services such as nutrient remediation while producing commercially valuable biomass. This study evaluates the performance of *Ulva ohnoi* cultivated in a seeded Algal Turf Scrubber (sATS), a land-based system designed to enhance cultivation control through reproductive cell inoculation. Fronds were collected from an aquaculture facility in Florianópolis, southern Brazil, induced to release reproductive cells, and inoculated at five distinct densities into sATS units operated under controlled conditions for 41 days. Growth parameters, including daily growth rate (DGR), frond morphology, and areal biomass productivity, were assessed alongside nutrient uptake kinetics for ammonium ($N–NH_4^+$) and phosphate ($P–PO_4^{3-}$). Results revealed that lower inoculation densities significantly improved cumulative DGR and frond length due to reduced intraspecific competition, while higher densities enhanced nutrient uptake efficiency and rate, particularly during the initial surge phase. Despite these contrasting responses, overall areal productivity remained stable across treatments (11.41 ± 1.41 g DW m^{-2} day^{-1}), while the system's capacity to respond to different inoculation densities highlights its potential for dual applications, either maximizing biomass yield or enhancing nutrient removal efficiency. When expressed as volumetric productivity, biomass production reached 0.96 g DW L^{-1} day^{-1}, surpassing most reported values and demonstrating high efficiency in water-limited culture systems. This result highlights the importance of coupling inoculation density with nutrient-supply strategies to overcome resource limitations and optimize system performance.

Keywords *Ulva ohnoi* · sATS · Algal Turf Scrubber · Bioremediation

Introduction

The cultivation of macroalgae, particularly *Ulva* spp., has been expanding not only due to the commercial value of its biomass (Toro-Mellado et al. 2025), but also because of the growing interest in cultivation systems that combine primary production with ecosystem services (Nobre et al. 2010; Luo et al. 2023). Within this context, *Ulva* is recognized as a promising genus for scalable biomass production, combining a high surface-to-volume ratio, efficient nutrient uptake, adaptability to a wide range of environmental conditions, and biomass rich in bioactive compounds, minerals, proteins, and soluble fibers (Salvi et al. 2021; Hofmann et al. 2024; Toro-Mellado et al. 2025; Zheng et al. 2025). These features make *Ulva* cultivation not only a viable biotechnological platform but also a sustainable tool to address global challenges related to food security, environmental management, and climate change mitigation (Gao et al. 2017a; Bhuyan et al. 2021).

Over the past decades, significant advances have been achieved in developing land-based cultivation systems for *Ulva* spp. (Mata et al. 2016; Praeger and de Nys 2017; Salvi et al. 2021). However, despite these advances, maximizing biomass production remains a challenge, as growth

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performance is strongly influenced by biological factors, such as reproductive biology and operational and abiotic parameters, including initial stocking density, nutrient supply, light intensity, and hydrodynamics (Carl et al. 2014; Praeger and de Nys 2018; Salvi et al. 2021; Robles-Carneiro et al. 2024). On the other hand, fine-tuning these parameters has proven to be essential for developing technological packages aimed at increasing productivity and/or improving the yields of target compounds (Msuya and Neori 2008; Salvi et al. 2021; Larsen-Ledet et al. 2025; Praeger et al. 2019).

Among the technologies recently developed for *Ulva* spp. cultivation, the seeded Algal Turf Scrubber (sATS) proposed by Salvi et al. (2021) represents an important advancement. The sATS is a modified variant of the ATS system initially developed by the Smithsonian Institution (Adey et al. 1996). Its main feature is the targeted inoculation of reproductive cells, which facilitates the establishment of monospecific cultures, reduces substrate colonization time, and minimizes interspecific competition (Salvi et al. 2021). This enhancement improves production control and system flexibility, making it suitable for diverse applications, ranging from effluent treatment to biomass production. Nevertheless, despite its advantages, sATS performance still depends on defining optimal conditions for critical operational parameters, particularly reproductive cell inoculation density, productivity and nutrient dynamics, and may ultimately determine long-term system stability. Bridging this knowledge gap is essential to scale the system beyond proof-of-concept trials and for consolidating its dual role as a platform for both macroalgal cultivation and bioremediation.

The use of *Ulva* spp. in bioremediation-based systems has gained increasing attention as a nature-based solution to removal of compounds, acting through the direct interception and assimilation of dissolved compounds before they reach critical concentrations (Copertino et al. 2009; Bastos et al. 2019b). Since the pioneering work of Neori and colleagues in land-based and integrated aquaculture systems (Neori et al. 1991, 2000, 2003), *Ulva* has been recognized as a multifunctional component capable of simultaneously improving water quality and generating valuable biomass. However, nutrient removal efficiency and biomass production are strongly dependent on operational parameters, particularly biomass density, often revealing a trade-off between growth performance and biofiltration efficiency. Lower biomass densities tend to favor higher specific growth rates and photosynthetic efficiency, whereas higher densities may enhance nutrient removal rates while constraining biomass production due to competition for light and nutrients (Msuya 2009; Massocato et al. 2022; Bao et al. 2024). These responses highlight the importance of fine-tuning cultivation parameters, such as inoculation density and nutrient supply, to balance biomass production and nutrient removal, a key challenge in optimizing land-based systems for both productive cultivation and bioremediation.

This study evaluates the performance of *Ulva ohnoi* cultivated in sATS (seeded Algal Turf Scrubber) units inoculated with reproductive cells at different densities. By assessing growth rates, morphological characteristics, and nutrient uptake dynamics ($N–NH_4^+$ and $P–PO_4^{3-}$), we provide insights into the biological and operational mechanisms that determine areal productivity in this system. Furthermore, by framing our results within the dual perspective of biomass production and bioremediation potential, we aim to advance the understanding of how simple adjustments in operational parameters can enhance the efficiency and versatility of sATS as a platform for sustainable macroalgae cultivation.

Materials and methods

Algal biomass collection and reproduction induction

Fronds of *Ulva ohnoi* were collected from an aquaculture facility in Florianópolis, Santa Catarina, Brazil (27° 35' 4.64" S; 48° 26' 31.10" W). In the laboratory the fronds underwent surface cleaning, which included washing sterilized seawater and baths of 20 s in distilled water and a 0.025% sodium hypochlorite solution to remove sediment, invertebrates, and epiphytes. The seawater was sterilized by mechanical filtering (5 and 10 µm) and exposed in continuous flow to UV-C irradiation. The algae used in this study originated from the same source as those taxonomically identified, both morphologically and molecularly, by Salvi et al. (2021).

To obtain reproductive cells, vegetative fronds were induced to gametogenesis/sporogenesis following Bastos et al. (2019a) with modifications. Vegetative fronds were fragmented with a chopper until fragments measured less than 3–5 mm^2. These fragments were washed four times with sterile seawater and recovered using a 100 µm mesh to remove all sporulation inhibitors. After washing, the fragments were exposed to air at 25 ºC for approximately 20 min and then rehydrated in culture medium composed of sterile seawater (salinity 35) enriched with a modified von Stosch nutrient solution (8 mL L^{-1}; nitrate replaced with ammonium (NH_4Cl), Ale et al. 2011). The fragments were maintained under controlled conditions with constant aeration, temperature of 25 ºC, irradiance of 100 ± 10 µmol photons m^{-2} s^{-1} and a 12-h photoperiod. After two days, reproductive cell release was observed, upon which the solution was filtered through a 100 µm mesh to remove frond fragments, and the reproductive cells concentrated using a 5 µm mesh. Cell density was then estimated using a Neubauer chamber. Three independent subsamples (1 mL each) were analyzed. When discrepancies among subsamples were observed, additional

samples were analyzed. The estimated density was then used for inoculation into the sATS system.

Seeded Algal Turf Scrubber (sATS)

The sATS system used was similar to that employed by Salvi et al. (2021) and comprises a ramp (60 cm long and 12 cm wide), connected to a 4.5-L reservoir (Fig. 1). The ramp is positioned at a 10° inclination, and circulation of the culture medium between the reservoir and the ramp was maintained by a pump operating at a flow rate of 1200 L h^{-1}. For reproductive cell fixation, a 1 mm mesh nylon screen was used as a substrate. Prior to ramp installation, the screen was submerged in fresh water for 24 hours and then rinsed under running fresh water.

Influence of reproductive cell density on growth rate and productivity

The influence of reproductive cell density on the growth rate and areal productivity of *U. ohnoi* cultivated in the sATS system was evaluated by inoculating 5 different initial densities of the reproductive cell and maintaining cultivation in the sATS system for 41 days. For this purpose, a solution of *U. ohnoi* reproductive cells was introduced into the sATS yielding final concentrations of 39 (C1), 116 (C2), 348 (C3), 1048 (C4) and 3142 (C5) reproductive cells per litre. Each concentration was tested in three independent sATS units ($n = 3$). Throughout the 41 days of cultivation, temperature was maintained at 25 ± 1 °C, and irradiance at 135 ± 10 µmol photons m^{-2} s^{-1} and a 12-h photoperiod was applied. The salinity was monitored daily and, when necessary, corrected with distilled water. Every two days, 8 mL L^{-1} of modified von Stosch nutrient solution was added and the culture medium (seawater and nutrient solution) was replaced every seven days. Starting on the 10th day post-inoculation, the substrate-algae assemblies were removed every 7 days and suspended for approximately 3 min to drain excess water before being weighed using an electronic balance (S2202H, Bel, Italy). Daily growth rates (DGR) were determined based on the increase in fresh biomass over time and calculated by the formula:

$$Daily\ Growth\ Rate\ (\%\ day^{-1}) = \left[\left(\frac{B_f}{B_i}\right)^{1/t} - 1\right] \times 100$$

where B_f is the final biomass, B_i is the initial biomass and t is the time in days.

The sATS areal productivity was calculated by the equation:

$$\text{Areal productivity}\left(g(DW)\ m^{-2}\ day^{-1}\right) = 0.2 \times \frac{\left(B_f - B_i\right)}{0.072}$$

where 0.2 represents the dry-to-fresh weight ratio and 0.072 m^2 is the surface area of the sATS ramp. To estimate the dry-to-fresh weight ratio used in areal productivity and nutrient-uptake calculations, *a posteriori* destructive sampling was performed. Biomass from all sATS units was homogenized and 30 sub-samples were randomly collected. Each subsample was weighed fresh, dried at 60 °C to constant weight (48–72 h), and weighed again. Frond length was determined by analyzing three randomly selected regions of the algal mat, each defined by a 3 × 3 cm^2. Within each region, 15 mesh threads were randomly selected. Along each thread, three points were randomly selected and all fronds attached

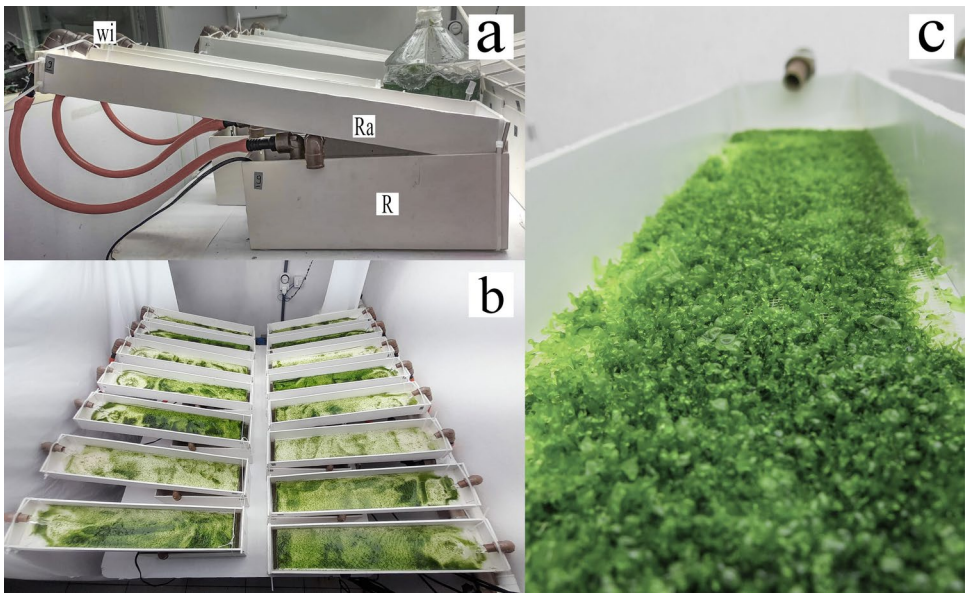


Fig. 1 Overview of the sATS cultivation system used in this study. **a** sATS system. R = reservoir, Ra = ramp and wi = water inlet. **b** 15 sATS systems after 10 days of maturation. **c** sATS system after 20 days of maturation

at these points were measured. For each frond, length was determined from the point of attachment on the mesh to the apex using ImageJ software (version 1.54g).

Effects of reproductive cell density on P-PO_4^{3-} and N-NH_4^+ removal

After 21 days of cultivation, nutrient-uptake kinetics for P-PO_4^{3-} and N-NH_4^+ were assessed. The assay was performed immediately after the routine weekly replacement of the culture medium, using the same modified von Stosch solution (VS) employed throughout the experiment. Thus, no additional nutrients were added beyond those normally supplied in the modified VS medium. Na_2HPO_4 and NH_4Cl were the phosphorus and nitrogen sources, respectively, within this standard medium, providing final concentrations of 2.35 mg L^{-1} of P and 7 mg L^{-1} of N. Immediately after medium replacement (t = 0), 6 mL samples were collected at 15, 30, 60, 120, 240, and 1440 minutes to quantify temporal changes in P-PO_4^{3-} and N-NH_4^+ concentrations. All measurements were conducted in triplicate ($n = 3$). The seawater used in the culture medium contained low nutrient concentrations, with N–NH_3/N–NH_4^+ and N–NO_3^- both below 0.1 mg L^{-1}, and P–PO_4^{3-} remaining undetectable. P-PO_4^{3-} was quantified using the molybdenum blue method according to Strickland and Parsons (1972), whereas N-NH_4^+ was analyzed via the indophenol method following Grasshoff et al. (1983). Additionally, initial 6 mL samples were taken prior to the addition of the modified von Stosch medium to determine baseline P-PO_4^{3-} and N-NH_4^+ concentrations. Based on the P-PO_4^{3-} and N-NH_4^+ measured concentrations, nutrient uptake efficiency (NUE) and nutrient uptake rate (NUR) were calculated according to the following equations:

$$\mathrm{NUE}(\%) = 100 - \frac{C_{t+1} \times 100}{C_t}$$

$$\mathrm{NUR}\left(\mathrm{mg\ g^{-1}(DW)\ h^{-1}}\right) = \frac{(C_t \times V_t) - (C_{t+1} \times V_{t+1})}{(B \times \Delta_t)}$$

where C_t represents the initial concentration, V_t the initial volume, C_{t+1} and V_{t+1} refer to the concentration and volume at the time point t+1, respectively, B is the dry biomass, and Δ_t is the time interval between t and t+1.

Statistical analysis

All data were tested for normality and homogeneity of variances using the Shapiro–Wilk and Cochran's tests, respectively. As both assumptions were met, parametric analyses were applied according to the structure of each response variable. To evaluate the effects of inoculated reproductive cell density over time, repeated measures ANOVA (RM-ANOVA) was performed for daily growth rate (DGR), areal productivity, phosphorus (P–PO_4^{3-}) and ammonium (N–NH_4^+) concentrations, nutrient use efficiency (NUE), and nutrient uptake rate (NUR). Time was treated as the repeated factor and inoculated reproductive cell density as the fixed factor. Main effects and time × density interactions were interpreted directly from the RM-ANOVA model. For analyses of P–PO_4^{3-} and N–NH_4^+ removal, the 1440-min sampling point was excluded because all treatments converged to nearly identical values, resulting in negligible between-treatment variation. Additionally, one-way ANOVA was used to evaluate the effect of inoculated reproductive cell density on cumulative DGR, cumulative areal productivity, and final thallus length measured at the end of the 41-day cultivation period. When significant differences were detected ($p < 0.05$), Student–Newman–Keuls (SNK) post hoc tests were applied following both RM-ANOVA and one-way ANOVA. For RM-ANOVA, comparisons were conducted among all time × density combinations when interactions were significant, or among significant main effects (time and/or density) when interactions were not significant. For one-way ANOVA, SNK tests were applied among treatment means. All analyses were performed using STATISTICA 12 and data are presented as mean ± standard deviation.

Results

The daily growth rates (DGR) of *U. ohnoi* seedlings cultivated in sATS systems with varying initial reproductive cells densities ($n = 3$) exhibited a pronounced decline over the experimental period, with an average decrease of 83.16 ± 4.2 % day^{-1} between the first (days 10 to 17) and fifth (days 38 to 41) week (RM - ANOVA: $F_{16,40} = 5.09$, $p < 0.001$; Fig. 2a). During the initial phase (days 10–17), the highest DGR values were recorded at the lowest densities, particularly in C1 (12.89 ± 0.94 % day^{-1}) and C2 (11.98 ± 1.07 % day^{-1}), both significantly higher than the other treatments (RM - ANOVA, SNK: $p < 0.001$; Fig. 2a and Table S1). In contrast, C3 (9.35 ± 0.23 % day^{-1}), C4 (8.59 ± 0.28 % day^{-1}), and C5 (7.87 ± 0.24 % day^{-1}) showed statistically similar values (RM - ANOVA, SNK: $p > 0.07$; Table S1). From the second week (days 17 to 24) onward, DGR values stabilized, averaging 3.85 ± 1.03 % day^{-1} (Fig. 2a and Table S1). Over the 31-day cultivation period, excluding the initial 10 days of inoculation, cumulative DGR varied significantly among the different reproductive cell densities (one-way ANOVA: $F_{4,10} = 12.26$, $p < 0.001$; Fig. 2b). The highest cumulative DGR values were observed in C1 (6.36 ± 0.14 % day^{-1}), while C5 presented the lowest value (4.46 ± 0.14 % day^{-1}), confirming an inverse relationship between the initial inoculated reproductive cell density and cumulative DGR (Fig. 2b).

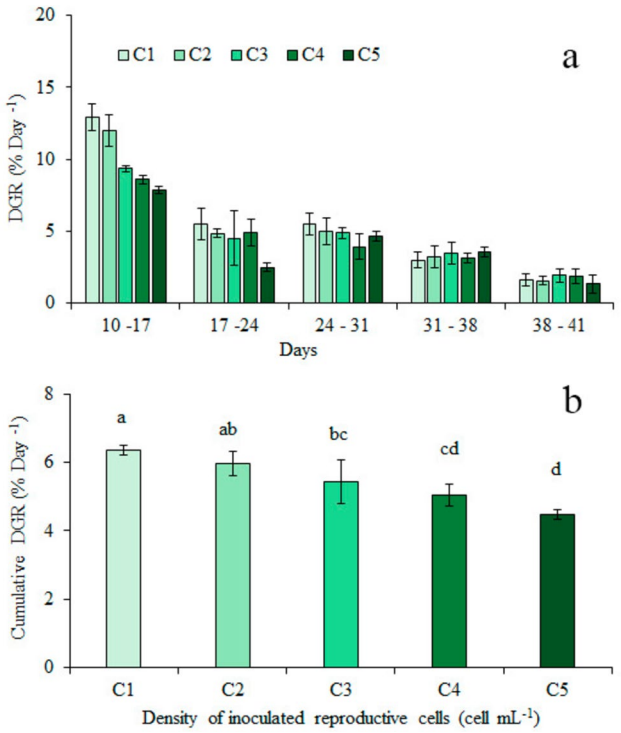


Fig. 2 Daily growth rate (DGR % day^{-1}) of *U. ohnoi* cultivated under different inoculated reproductive cell densities (C1: 39; C2: 116; C3: 348; C4: 1048; C5: 3142 cells mL^{-1}). (**a**) DGR over time. A significant interaction between time and treatment was detected (RM - ANOVA, $p < 0.001$). Therefore, letters (Table S1) represent post hoc comparisons among all time x treatment combinations (SNK, $p < 0.05$). (**b**) Cumulative DGR between days 10 and 41. Different letters indicate statistically significant differences among treatments (one-way ANOVA, $p < 0.001$; SNK post hoc test, $p < 0.05$). Data represent mean ± standard deviation ($n = 3$)

Weekly productivity data revealed no significant interaction between inoculated reproductive cell density and time (RM - ANOVA: $F_{16,40} = 1.116$, $p = 0.373$; Fig. 3a), and no significant main effect of reproductive cell density (RM - ANOVA: $F_{4,10} = 2.123$, $p = 0.152$; Fig. 3a). In contrast, a significant main effect of time was detected (RM - ANOVA: $F_{4,40} = 7.730$, $p < 0.001$; Fig. 3a), indicating that productivity varied over time similarly across all treatments. Overall, productivity remained relatively stable throughout the cultivation period, with an average of 11.03 ± 2.78 g DW m^{-2} day^{-1}. Post hoc SNK comparisons showed that productivity during days 17–24 was significantly lower than during days 10–17, 24–31, 31–38, and 38–42 ($p < 0.01$; Fig. 3a). No significant differences were detected among the remaining time intervals ($p > 0.05$). Final cumulative productivity averaged 11.41 ± 1.41 g DW m^{-2} day^{-1}, with no significant differences among the initial inoculated reproductive cell densities. (one-way ANOVA: $F_{4,10} = 2.37$, $p = 0.12$; Fig. 3b).

At the end of the experiment (41 days), the frond lengths of *U. ohnoi* varied significantly across the different inoculated densities of reproductive cells (one-way ANOVA: $F_{4,10} = 5.16$, $p = 0.02$; Fig. 4 and 5). Overall, longer fronds were observed at lower inoculation densities, with C1, C2, and C3 reaching 0.60 ± 0.049 cm, 0.54 ± 0.12 cm, and 0.47 ± 0.11 cm lengths, respectively, with no significant differences among them (one-way ANOVA, SNK: $p > 0.20$; Fig. 4 and 5c). The shortest frond lengths were observed in the higher-density treatments, C4 (0.37 ± 0.09 cm) and C5 (0.31 ± 0.03 cm), which also did not differ significantly from each other (one-way ANOVA, SNK: $p = 0.46$; Fig. 4 and 5).

After 21 days of reproductive cell inoculation, nutrient uptake kinetics were assessed using known concentrations of P-PO_4^{3-} and N-NH_4^+ ($n = 3$). Variations in nutrient concentrations, as well as nutrient uptake efficiency (NUE) and nutrient uptake rate (NUR), are shown in Figs.6a, b and c and 7a, b and c. In general, over the 1440 min incubation period, both nutrients showed a marked decline; however, the decrease in P-PO_4^{3-} occurred more gradually during the first 240 min, while N-NH_4^+ exhibited consistently sharper reductions throughout the entire incubation period, with both nutrients approaching complete removal by 1440 min (Figs. 6a and 7a).

For P–PO_4^{3-}, RM - ANOVA detected no significant interaction between time and inoculated reproductive cell density ($F_{16,40} = 0.483$, $p = 0.941$; Fig. 6a). Significant main effects were observed for inoculated reproductive cell density ($F_{4,10} = 14.689$, $p < 0.001$) and time ($F_{4,40} = 121.122$, $p < 0.001$). P–PO_4^{3-} concentrations decreased from 15 to 240 min in all treatments (Fig. 6a; Table S2). Mean concentrations differed among densities, with C5 presenting the lowest values and C2 the highest. (Fig. 6a and Table S2). Nutrient use efficiency (NUE; Fig. 6b) showed no significant interaction between time and inoculated reproductive cell density according to RM - ANOVA ($F_{16,40} = 0.483$, $p = 0.941$). Significant main effects were observed for both inoculated reproductive cell density ($F_{4,10} = 14.689$, $p < 0.001$) and time ($F_{4,40} = 121.121$, $p < 0.001$). The highest NUE values were observed for C5 (59.24 ± 7.46%; RM - ANOVA, SNK: $p < 0.01$ and Table S2). NUR values (Fig. 6c) were significantly influenced by the interaction between time and the density of inoculated reproductive cells (RM - ANOVA = $F_{16,40} = 8.728$, $p < 0.001$; Fig. 6c), The maximum NUR values were observed at 30 min for C5 (0.759 ± 0.139 mg P-PO_4^{3-} g^{-1} DW h^{-1}) and C4 (0.560 ± 0.080 mg P-PO_4^{3-} g^{-1} DW h^{-1}), with no significant differences between them (RM - ANOVA, SNK: $p < 0.01$; Fig. 6c and Table S2). After 60 min, no statistically significant differences were detected among treatments (RM - ANOVA, SNK: $p > 0.05$ and Table S2). Similarly, for N-NH_4^+, an inverse relationship was observed between reproductive cell density and residual concentrations at higher densities (C5 and C4; Fig. 7a). N-NH_4^+ removal was influenced by the interaction of reproductive cell density and time (RM - ANOVA = $F_{16,40} = 8.362$, $p < 0.001$; Fig. 7a and Table S3). The NUE and NUR

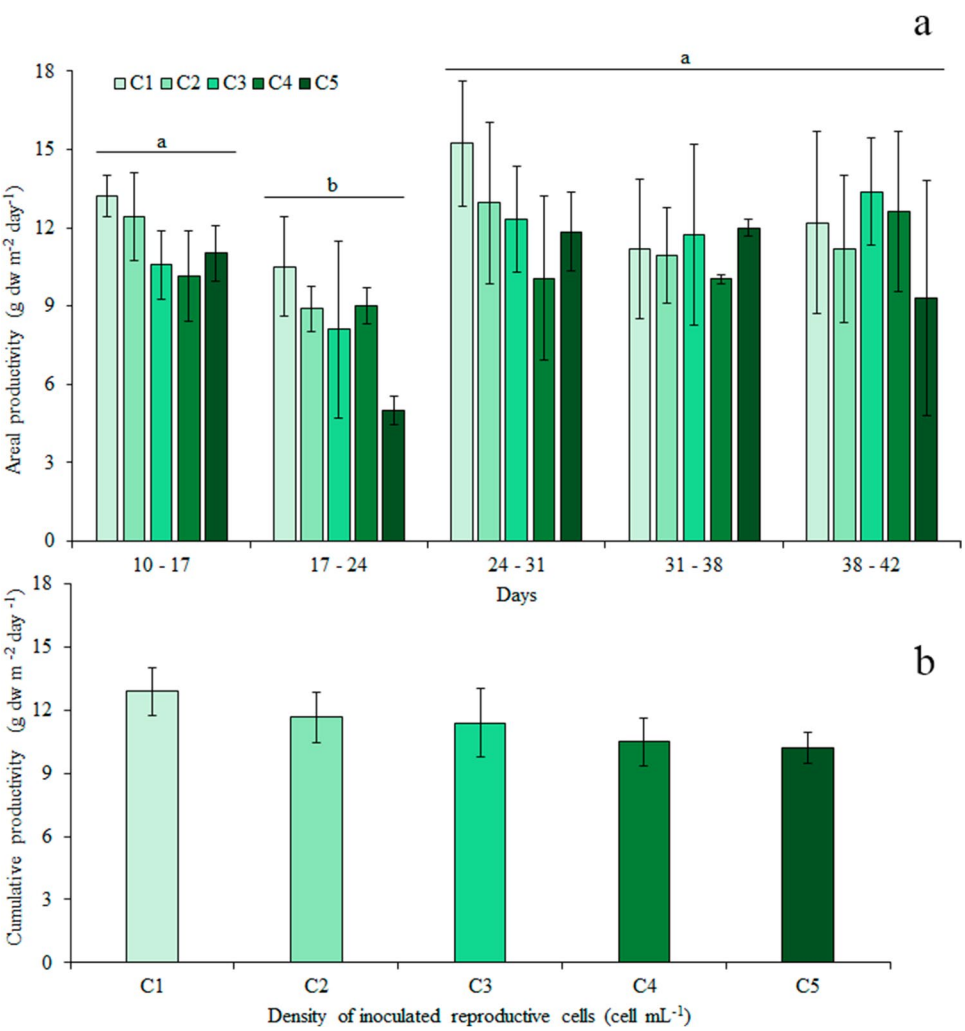


Fig. 3 Productivity (g DW m^{-2} day^{-1}) of *U. ohnoi* cultivated under different reproductive cell inoculation densities (C1: 39; C2: 116; C3: 348; C4: 1048; C5: 3142 cells mL^{-1}). (**a**) Productivity over time. No significant interaction between time and treatment was detected (RM - ANOVA, $p = 0.373$), and no effect of treatment was observed ($p = 0.152$). A significant main effect of time was detected ($p < 0.001$); therefore, letters indicate statistically significant differences among time points (SNK, $p < 0.05$). (**b**) Cumulative productivity between days 10 and 41. No significant differences among treatments were detected (one-way ANOVA, $p = 0.121$). Data represent mean ± standard deviation ($n = 3$)

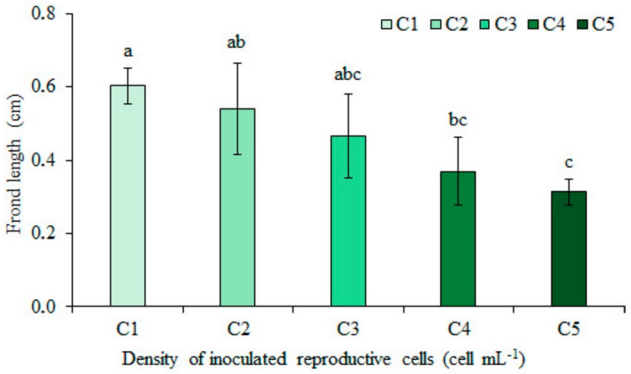


Fig. 4 Frond length (cm) of *U. ohnoi* cultivated under different reproductive cell inoculation densities (C1: 39; C2: 116; C3: 348; C4: 1048; C5: 3142 cells mL^{-1}) at the end of the experimental period (41 days). Significant differences among treatments were detected (one-way ANOVA, $p = 0.016$). Different letters indicate statistically significant differences among treatments (SNK post hoc test, $p < 0.05$). Data represent mean ± standard deviation ($n = 3$)

values varied between the initial reproductive cell densities and time (RM - ANOVA: NUE = $F_{16,40} = 8.360$, $p < 0.001$; NUR = $F_{16,40} = 6.736$, $p < 0.001$; Fig. 7b, e, c and Table S3). In the first 15 minutes, the highest NUE values for $N\text{-}NH_4^+$ (RM - ANOVA, SNK, $p < 0.001$ and Table S3) was observed for C5 (72.29 ± 3.73%), reaching 92.69 ± 2.44% after 30 minutes (RM - ANOVA, SNK, $p < 0.001$ and Table S3). NUE values above 90% were observed at 120 min for C4 (93.25 ± 0.96%) and 240 min for C1 (96.96 ± 0.15%), C2 (92.87 ± 1.20%) and C3 (94.30 ± 0.79%), when the treatments did not differ statistically from each other (RM - ANOVA, SNK, $p > 0.30$ and Table S3). NUR values for all initial reproductive cell densities increased between 15 and 30 min, followed by a consistent decline at all subsequent time points (Fig. 7c). The highest NUR was observed in C5 (26.63 ± 1.63 mg $N\text{-}NH_4^+$ g^{-1} DW h^{-1}), followed by C4 (23.26 ± 3.36 mg $N\text{-}NH_4^+$ g^{-1} DW h^{-1}), C3 (21.20 ± 3.33 mg $N\text{-}NH_4^+$ g^{-1} DW h^{-1}) and C1 (20.65 ± 0.93 mg $N\text{-}NH_4^+$ g^{-1} DW h^{-1}), with no statistically significant differences among treatments (RM - ANOVA, SNK, $p > 0.07$; Fig. 7c and Table S3).

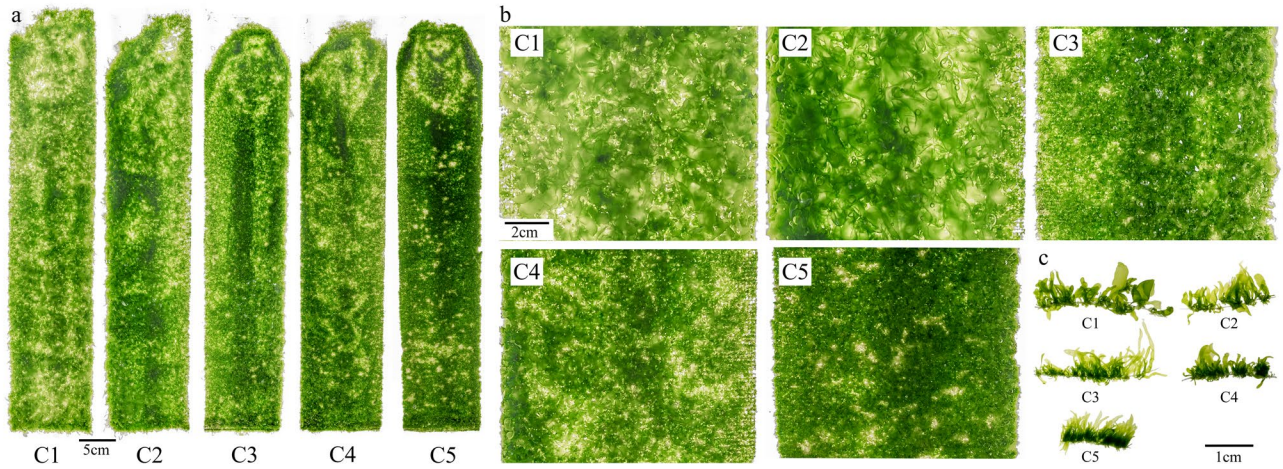


Fig. 5 *U. ohnoi* frond development under different reproductive cell inoculation densities (C1: 39; C2: 116; C3: 348; C4: 1048; C5: 3142 cells mL^{-1}) at the end of the experimental period (41 days). **a** Appearance of the substrate after 41 days of cultivation of *U. ohnoi* under different reproductive cell inoculation densities (C1: 39; C2: 116; C3: 348; C4: 1048; C5: 3142 cells mL^{-1}). **b** Appearance of the fronds and substrate coverage. **c** Frond length

Discussion

The findings of this study demonstrate that the functionality of the sATS system can be strategically modulated through adjustments in reproductive cell inoculation density, significantly influencing key performance parameters such as frond length, daily growth rate (DGR), and nutrient (N and P) uptake dynamics. Lower inoculation densities, as observed in C1, reduced intraspecific competition, leading to a 48% increase in frond length and a 30% increase in DGR when compared to higher-density treatments such as C5. In contrast, higher initial densities (e.g., C5) led to greater nutrient removal efficiencies, with N-NH_4^+ and P-PO_4^{3-} uptake rates being 22% and 13% higher, respectively, than those observed in C1. The complete removal of nutrients within 24 hours across all treatments indicates that the system operated below its maximum nutrient uptake capacity, with no signs of saturation in response to the nutrient concentrations added during the cultivation period. This translated into increased nitrogen and phosphorus utilization rates (NUR and NUE), highlighting the suitability of higher-density inoculation for bioremediation purposes. The dual nature of these responses underscores the system's operational plasticity, allowing for the fine-tuning of inoculation strategies according to specific cultivation objectives, whether maximizing biomass production or enhancing nutrient removal efficiency. Thus, the results of this study constitute a significant advancement of the proof of concept initiated by Salvi et al. (2021), aimed at optimizing the sATS system.

In this context, our DGR values were comparable to those reported for species of *Ulva*, such as *U. fasciata* (Mantri et al. 2011), *U. flexuosa* and *U. linza* (Cardoso et al. 2023), and lower than those observed for *U. ohnoi* (Bastos et al. 2019a), all cultivated in vitro using reproductive cells as inocula. Furthermore, our results were 2.7 times higher than those obtained by Salvi (2021) for *U. ohnoi* using the sATS system under the same methodological approach. When compared with studies employing frond fragments as inoculum, our DGR values were higher than those reported for *Ulva* sp. cultivated in photobioreactors (Pasquini et al. 2024), *U. compressa* in raceways (Robles-Carnero et al. 2024), and *U. ohnoi* cultivated in vitro (Bastos 2019b), although lower than those observed for *U. lactuca* in CO_2-supplemented photobioreactors (Savvashe et al. 2021). However, these differences cannot be attributed solely to the cultivation system as inoculum density, nutrient availability, and other methodological factors likely also contributed to the observed productivity patterns.

Reproductive cell inoculation density strongly influenced DGR, with an inverse relationship particularly evident during the first two weeks of cultivation. This pattern is consistent with previous studies identifying initial cell density as a central factor regulating biomass production in *Ulva* spp. cultures (Carl et al. 2014; Praeger and de Nys 2017; Salvi et al. 2021; Steinhagen et al. 2022), although responses are often non-linear and vary according to species and cultivation system. For example, sea-based farming systems using higher initial inoculation densities, typically preceded by a nursery phase, have proven effective in maximizing total biomass yield (Carl et al. 2014; Steinhagen et al. 2021), whereas in land-based systems intraspecific competition may develop earlier (Bastos et al. 2019a; Salvi et al. 2021). These contrasting outcomes are likely related to hydrodynamic conditions in open-water environments, which enhance nutrient renewal, reduce self-shading, and disrupt boundary layers.

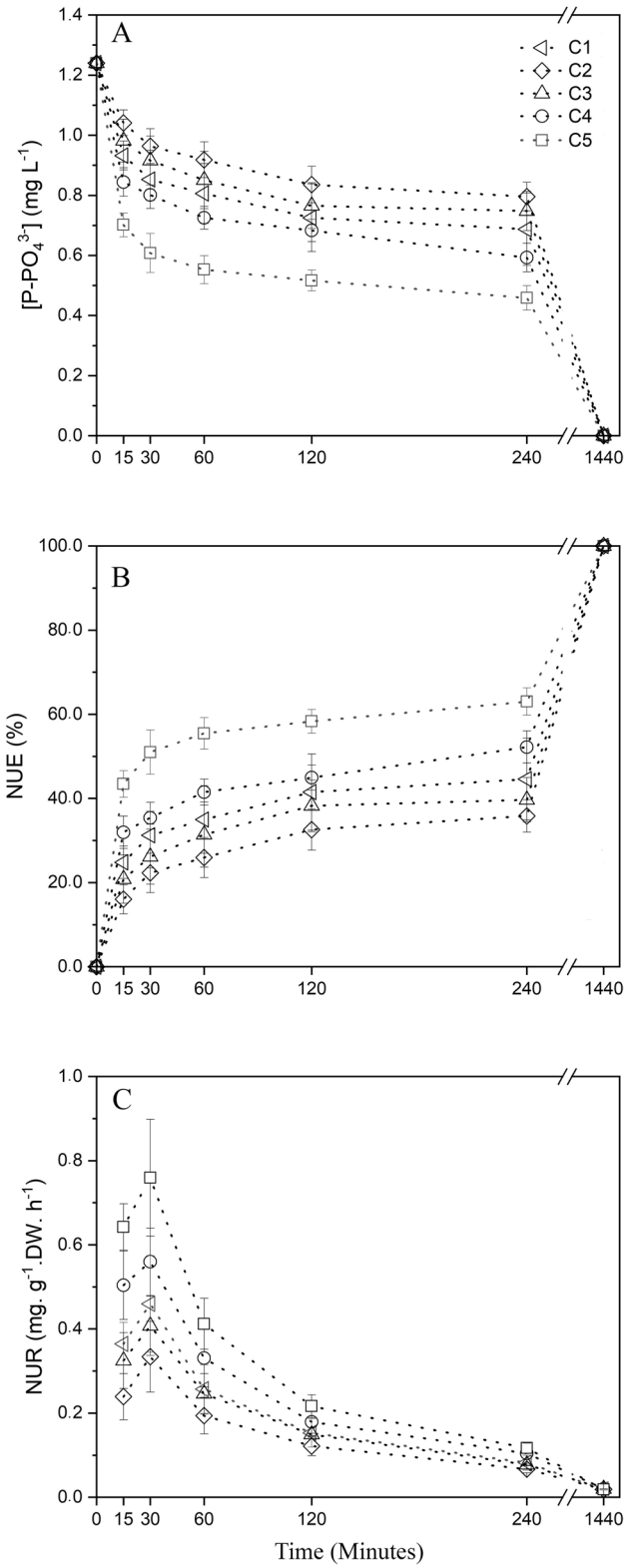


Fig. 6 a- Phosphorus dynamics in *U. ohnoi* cultivated under different reproductive cell inoculation densities (C1: 39; C2: 116; C3: 348; C4: 1048; C5: 3142 cells mL^{-1}). **a** Changes in concentrations of $P\text{-}PO_4^{3-}$ (mg L^{-1}), **b** removal rate (NUR) and **c** uptake efficiency (NUE). Data represent the mean ± standard deviation for $n = 3$. Results of the post hoc SNK test are in Table S2

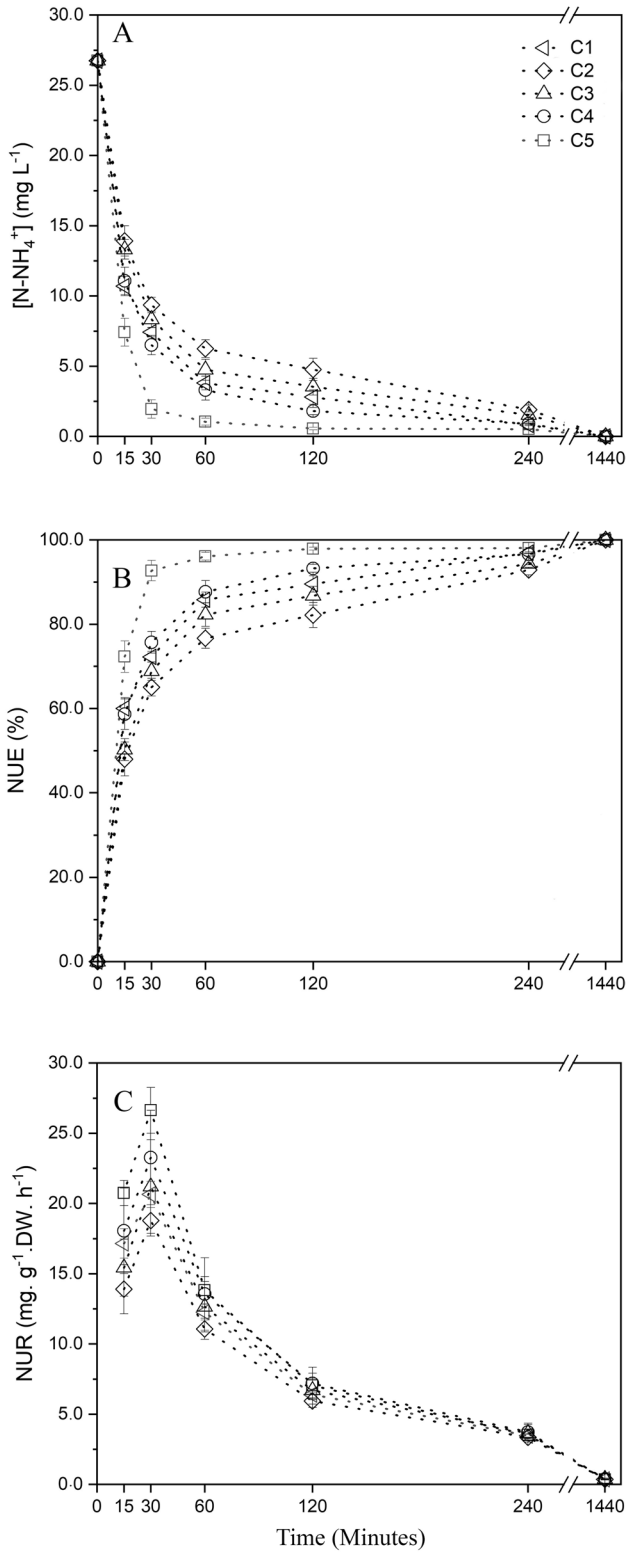


Fig. 7 Ammonium dynamics in *U. ohnoi* cultivated under different reproductive cell inoculation densities (C1: 39; C2: 116; C3: 348; C4: 1048; C5: 3142 cells mL^{-1}). a- Changes in concentrations of $N\text{-}NH_4^+$ (mg L^{-1}), b - removal rate (NUR) and C - uptake efficiency (NUE). Data represent the mean ± standard deviation for $n = 3$. Results of the post hoc SNK test are in Table S3

In addition to inoculation density, cultivation duration may also influence productivity. Under both sea and land-based conditions, prolonged cultivation often results in reduced growth rates and productivity due to frond maturation, which increases the frequency of reproductive events and can lead to biomass degradation as vegetative cells differentiate into reproductive cells and spore release ruptures the cell wall (Oza and Sreenivasa 1977; Gao et al. 2017b; Steinhagen et al. 2022). Although not quantified, reproductive events were observed in all treatments from approximately 20 days after inoculation. In this context, periodic partial harvesting of fronds while maintaining the holdfast for regrowth may represent an effective management strategy. Previous studies indicate that more frequent harvesting, particularly on a weekly basis, can stimulate growth and biomass productivity in *Ulva* (Castelar et al. 2014; Carl et al. 2016). Therefore, regular harvesting may help maintain productive biomass, reduce crowding, and limit losses associated with tissue aging and reproduction (Steinhagen et al. 2022).

Thallus length was also inversely related to reproductive cell inoculation density, suggesting that reduced crowding at lower initial densities favored greater individual development. This pattern has also been reported in other studies in species such as *U. intestinalis* (Ruangchuay et al. 2012) and *U. ohnoi* (Silva et al. 2024), suggesting that lower inoculation densities promote more efficient per-individual resource allocation, particularly in terms of light and nutrients availability. Recent experimental evidence reinforces that low stocking densities under high light conditions significantly enhance growth rates, photosynthetic efficiency, and nutrient absorption in *U. linza* (Bao et al. 2024), whereas high densities suppress these parameters, probably due to increased competition. These physiological constraints likely contribute to the inversely proportional response observed in this study between frond length and inoculated reproductive cell density. Importantly, despite significant differences in frond length across treatments, total productivity remained constant. This indicates a compensatory mechanism whereby, under lower inoculation densities, the increase in frond length offsets the reduced abundance of individuals, thereby maintaining overall productivity. Conversely, it suggests that the sATS system, under the tested configurations, has not yet reached its full potential for biomass production by *U. ohnoi*. Thus, fine-tuning reproductive cell inoculation density in conjunction with culture conditions, including nutrient supply, light intensity, and flow-rate, represents a key approach to minimizing resource constraints at the individual level and maximizing system productivity.

The productivity observed in this study, ranging from 10.19 to 12.89 g DW m^{-2} day^{-1}, falls within the lower–middle range when compared with the mean values reported in other studies on *Ulva* spp. (Table 1), conducted at pilot or commercial scales. It is important to note, however, that such direct comparisons are limited by methodological differences, including nutrient composition and flow rate, abiotic parameters, water exchange rates, cultivated species, and initial stocking densities. Nevertheless, the system employed here, despite being at a laboratory scale, demonstrates considerable potential, as it required only 4.5 L of seawater in operation (22.5 L over a 41-day production cycle from inoculation) per system, occupying an area of 0.072 m^2. When converted to g L^{-1} day^{-1}, based on the operational volume, the productivity obtained (0.96 g FW L^{-1} day^{-1}) exceeds most values reported in the literature (Table 1), highlighting the system's efficiency in terms of both water use and biomass production, and suggesting its applicability in contexts where seawater availability and space are limiting factors.

Table 1 Comparative summary of cultivation conditions and volumetric and areal productivity of *Ulva* spp. in land-based systems

Species	Water Volume (L)	Water Exchange (L day^{-1})	Stocking Density (kg FW m^{-2})	Volumetric Productivity (g L^{-1} day^{-1})	Areal Productivity (g DW m^{-2} day^{-1})	References
U. ohnoi	4.5	0.72	-	0.96	11.03	This stud
U. ohnoi	3	0.36	-	0.40	3.8	Salvi et al. 2021
U. compressa	3000	0	0.6 - 1	0.37 - 0.48	6.23 - 8	Robles-Camero et al., 2024
U. lactuca	800	0	1 - 3	0.32 - 0.17	25 - 13	Shpigel et al. 2019
U. lactuca	600	34	1	0.19 - 0.63	11 - 38	Msuya and Neori 2008
U. reticulata	40	2040	1	l.35 - 2.3	46	Msuya et al. 2006
U. rigida	750	2 -12	2.5	0.09 - 0.32	40	Rio et al, 1996
U. lactuca	600	4 - 16	2 - 6	0.24 - 0.42	55	Neori and Gordin, 1991
U. lactuca	600	12	1 - 8	0.37 - 0.16	12.32	Bruhn et al 2010
U. lactuca	600	2	1.5	0.39	21.3	Neori et al. 2000
U. latuca	900–1700	14 - 56	1	0.26 - 0.64	19	Neori et al. 2003

Ranges indicate variability associated with cultivation parameters within each study. Modified from Shpigel et al. 2019

When analyzing the nutrient uptake data, it became evident that nutrient availability was the main limiting factor for biomass production by *U. ohnoi* in the sATS system. Despite differences in inoculation densities, both $P–PO_4^{3-}$ and $N–NH_4^+$ were completely depleted across all treatments, indicating that the supplied concentrations were insufficient to sustain higher productivity. The rapid decrease in nutrient concentrations observed, particularly in the first 15–30 min at higher densities (C4–C5), aligns with the well-described phenomenon of surge uptake in *Ulva* spp., where a short-lived phase of accelerated assimilation is followed by stabilization at lower, maintenance rates (Pedersen 1994; Raikar and Wafar 2006; Lubsch and Timmermans 2017). This response is further explained by the morphological traits of the genus *Ulva*, whose high surface-to-volume ratio confers not only elevated photosynthetic rates and efficient carbon fixation but also favors accelerated nutrient absorption (Stewart and Carpenter 2003; Chen et al. 2019). Consequently, although higher inoculation densities enhanced early uptake efficiency (higher NUE and NUR), the uniform depletion of nutrients across all treatments ultimately constrained growth. Comparable results have been reported in land-based raceway and sATS systems, where *Ulva* spp. rapidly exhaust dissolved inorganic nitrogen and phosphorus when external supply is low, thereby limiting biomass accumulation (Salvi et al. 2021; Massocato et al. 2022; Robles-Carnero et al. 2024). Thus, these results demonstrate that nutrient supply, rather than inoculation reproductive cell density alone, was the decisive factor driving productivity in our system. Therefore, to overcome limiting factors and enhance *U. ohnoi* biomass production in sATS, optimization must couple inoculated reproductive cell density with nutrient supply strategies, whether pulsed, semi-continuous, or scaled with biomass accumulation, to prevent premature resource depletion.

Viewed through the lens of bioremediation, the rapid and complete removal of both $N–NH_4^+$ and $P–PO_4^{3-}$ by *U. ohnoi* in the sATS system highlights its potential as a cultivation platform for nutrient removal and water quality improvement under controlled conditions. The use of *Ulva* spp. for nutrient removal is well documented in aquaculture (Hernández et al. 2002; Shpigel et al. 2019) and sewage effluents (Tsagkamilis et al. 2010). For instance, Copertino et al. (2009) reported that *U. clathrata*, cultivated in shrimp aquaculture effluents, reduced dissolved inorganic nitrogen (82%) and phosphorus (50%) within short timeframes. Similarly, Salvi et al. (2021) observed rapid depletion of $N–NH_4^+$ and $P–PO_4^{3-}$ in sATS systems seeded with *U. ohnoi*, with uptake rates reaching up to 2.511 mg $N–NH_4^+$ g^{-1} DW h^{-1} and 73.626 mg $P–PO_4^{3-}$ g^{-1} DW h^{-1}. However, differences in nutrient concentrations, biomass density, and system configuration across studies limit direct comparisons. In the present study, nutrient levels were relatively low, and rapid depletion likely reflects the balance between nutrient availability and biomass demand. These results therefore indicate the system's capacity for nutrient uptake under these conditions, while suggesting its potential for application under a broader range of nutrient regimes, which should be further evaluated in targeted studies.

Finally, this study demonstrates that the initial density of reproductive cells of *U. ohnoi* is a key factor governing the functional performance of the sATS, directly influencing morphological traits, biomass productivity, and the removal of $P–PO_4^{3-}$ and $N–NH_4^+$. The system's capacity to flexibly respond to different inoculation densities underscores its high potential for dual applications, either maximizing biomass yield or enhancing nutrient removal efficiency. Thus, sATS emerges as a versatile platform, allowing fine-tuned adjustments through simple operational variables such as inoculation density, thereby enabling optimization according to specific cultivation goals. These results highlight the importance of integrated approaches combining biology and systems engineering in the development of sustainable and effective solutions for macroalgal cultivation and bioremediation.

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Authors' contributions Luana de Azevedo Aimi: conception or design of the work; data acquisition; analysis; interpretation of data; drafted the work or revised it critically for important intellectual content. Milena Drehmer Menezes: data acquisition; interpretation of data; drafted the work. Christine Abreu Oliveira: data acquisition; interpretation of data; drafted the work. Santos Gonçalves Magagin: data acquisition; interpretation of data; drafted the work. Paulo Antunes Horta: conception or design of the work; analysis; interpretation of data; drafted the work or revised it critically for important intellectual content. Leonardo Rubi Rörig: conception or design of the work; interpretation of data; drafted the work or revised it critically for important intellectual content. Eduardo Bastos: conception or design of the work; data acquisition; analysis; interpretation of data; drafted the work or revised it critically for important intellectual content. All authors approved the version to be published; and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Data availability The data that support the findings of this study are available from the corresponding author, EB, upon request.

Declarations

Competing interests The authors declare no competing interests.

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