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RESEARCH

Resilience of the red alga *Palmaria palmata* to anthropogenic environmental changes: Small-scale flask assessment of combined effects of marine heatwaves, hyposalinity, and marine pollution

Pierre Liboureau[1] · Renan Monte de Oliveira[2] · Lísia Mônica de Souza Gestinari[2] · Daniela Maria Pampanin[1]

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Abstract
Seaweeds are keystone species supporting ecosystems and human activities. Despite their vulnerability to increasing anthropogenic pressures, multi-exposure experiments with macroalgae are rare, especially in non-kelp species. This study examined the combined effects of marine heatwaves (+ 3℃; MHW), hyposalinity (-8 PSU; Sal), and wastewater treatment plant effluent (WWTP) in *Palmaria palmata* (Rhodophyta), representative of present and projected environmental changes. Sporulating and vegetative blades were exposed to single and combined stressors for two weeks, followed by one week (sporulating) and six weeks (vegetative) of recovery. Growth (fresh weight, surface area) and photosynthetic ability (maximum quantum yield of PSII, F_v/F_m; maximum electron transport rate, $rETR_{max}$) were measured weekly to assess effects on the health and development of the blades. Final blade size did not differ significantly between exposures in vegetative blades despite temporarily increased growth rates. In sporulating blades, MHW and WWTP led to 1.8-fold larger blades than controls. F_v/F_m decreased during MHW, Sal+WWTP, Sal+MHW, and WWTP+MHW exposures (1.4-fold), indicating transient stress. No lasting effects were observed after recovery. The $rETR_{max}$ was unaffected by exposures and increased steadily over time. Photosynthetic measurements suggest some level of stress during exposures, accompanied by compensation mechanisms in response to PSII damage. The temporary increases in growth rates may indicate hormetic mechanisms with potential for adaptive plasticity, although selected MHW and Sal exposures are within the natural range of *P. palmata*, and sudden changes did not cause long-term stress in vegetative thalli. These outcomes highlight the resilience of wild and cultivated *P. palmata*.

Keywords Rhodophyta · Stress · Climate change · Hormesis · Plasticity · Reproductive thallus

Introduction

Seaweeds are the most widespread habitat-forming species in coastal ecosystems, providing a range of ecological functions, including food and shelter provisioning, sediment stabilisation, pH buffering, and nutrient cycling (Machado and Oliveira 2024). They also support many ecosystem services and have been used directly and indirectly by humans for millennia (Mouritsen et al. 2021; Cotas et al. 2023). Furthermore, interest in seaweed cultivation as a sustainable source of food, as well as other valuable compounds, such as colloids and nutraceuticals, is rising globally (Wang et al. 2025). However, as sessile, autotrophic organisms absorbing nutrients from seawater, seaweeds are particularly vulnerable to sudden environmental changes and aquatic pollutants (Contreras-Porcia et al. 2017; Segaran et al. 2023; Yadav and Mantri 2025). Research into climate change and pollution effects on seaweeds has increased in recent years, with a general focus on seawater warming, acidification, and specific polluting compounds (e.g., heavy metals). On the other hand, changes in seasonal climate patterns and general pollution loads are poorly understood despite their relevance for large populations and ecosystems. Multi-exposure experiments also remain scarce but have long been considered key to improving management and regulations in ecotoxicology (Orr et al. 2024). Finally, most research has so far focused on larger, keystone kelps, despite the foundational role of

✉ Pierre Liboureau
pierre.e.liboureau@uis.no

[1] Department of Chemistry, Bioscience and Environmental Engineering, University of Stavanger, 4036 Stavanger, Norway

[2] Institute of Biodiversity and Sustainability, Federal University of Rio de Janeiro, Rio de Janeiro, Brazil

other species in helping to structure the habitat and provide a range of functions and services (Cotas et al. 2023; Farrugia Drakard et al. 2023).

Palmaria palmata is a foliose red alga widespread in the North Atlantic at latitudes ranging from Portugal to the Arctic (Stévant et al. 2023). It contributes to structuring varied ecosystems, being both epiphytic, typically growing on larger kelp stipes, and epilithic, present in rocky inter- and subtidal environments (Florez et al. 2017; Dumay et al. 2022). Traditionally harvested and eaten through much of its range, the high protein content and strong bioactive potential make this species an ideal candidate for the development of aquaculture (Grote 2019; Liboureau and Pampanin 2024). Reproduction in *P. palmata* is seasonal, with sporulation happening exclusively in winter and early spring, and has heteromorphic alternation of generations (van derMeer and Todd 1980). Male gametophytes grow to full macroscopic size for a year before reproducing with microscopic, crustose females produced during the next sporulation year. This process relies on environmental triggers for synchronisation of the life stages, with no known hormonal communication. Physiological and molecular disruptions may therefore lead to reproductive failures and potentially widespread damage to populations. Nonetheless, few studies have examined the potential vulnerability of *P. palmata* to existing and emerging anthropogenic environmental changes.

Surface seawater temperatures (SST) are expected to increase in the North Sea by 2 ºC within 40–70 years, depending on climate change scenarios (Ottersen et al. 2023). Additionally, marine heatwaves have increased in frequency and intensity in the region over the last two decades, with winter temperature increases of up to 3 ºC (Mohamed et al. 2023). Decreases in salinity are frequently recorded due to increased freshwater runoff, both from heavy rainfall and snow melt in spring in the North Sea (Núñez-Riboni and Akimova 2017). On the French Atlantic coast, salinity decreased by up to 12 PSU during extreme events, but sustained hyposaline conditions were typically up to −8 PSU (Poppeschi et al. 2021). Despite good overall water quality in the North Sea, wastewater treatment plant effluents (WWTPE) are ubiquitous near inhabited areas. Many potentially toxic chemicals remain in the effluent after treatment, and their constant output may present a hazard for ecosystems in large regions around the outlet (Pampanin et al. 2024).

In this study, both vegetative and sporulating blades of *P. palmata* were exposed to individual and combined environmental change events, including hyposalinity, marine heatwaves, and pollution from WWTPE, using growth and photosynthetic activity to evaluate effects during exposures and after recovery. We hypothesised that i) short exposures to sudden changes in environmental conditions and WWTPE deteriorate the health and growth of *P. palmata*; ii) multi-exposures may have synergistic effects and lead to increased damage; and iii) reproductive thalli are more susceptible to short-term environmental disruptions.

Materials and methods

Algal material

Both vegetative and sporulating *Palmaria palmata* thalli were sampled from a wild population in Vistnes, Norway (58.983 ºN, 5.569 ºE), on 31 March 2025 (salinity 30.9 PSU, SST = 4.8 ℃, t = −3d). For each reproductive stage (i.e., vegetative or sporulating), 20 individuals were sampled by swimming at 0–2 m depth (low tide) in a ~0.01 km^2 subtidal area to obtain ~2 kg of biomass (fresh weight, FW). Each thallus was sampled from a unique rock or kelp substratum, following a serpentine pattern. Only individuals with a blade length of > 10 cm were selected, and only a part of the whole thallus was harvested to obtain ~100 g FW while limiting impacts on the local population. F/2 medium was used throughout this study (100%; Guillard 1975; nutrient mix acquired from Varicon Aqua, UK), based on artificial seawater (ASW), with a salinity of 32 ± 0.5 PSU (Instant Ocean Salt, Aquarium Systems, France). ASW was used to ensure control over the salinity, nutrient levels, and potential presence of pollutants in the water.

Specimens were cleaned of visible fouling and epiphytes, rinsed in ASW and placed in 5-L flat-bottom flasks containing F/2 medium with aeration, 30 µmol photons m^{-2} s^{-1} light (TLD 36W/840; Philips, Netherlands), 12h:12h light:dark (L:D) cycle, corresponding to light conditions in April in the area, in an incubator (MLR-352-PE, PHCbi, Japan). The initial temperature of 5 ℃ was increased by 1 ℃ every 12 h until it reached 7 ℃, based on average SSTs in April (SeaTemperature.org). These conditions were used for acclimation, control, and recovery during the experiment. *P. palmata* thalli were acclimated for 48 h (until t = −1 day) before cutting two individual blades from each individual, averaging 549 ± 34 mg and 2114 ± 118 mm^2 (n = 40) for vegetative blades, and 777 ± 55 mg and 2638 ± 159 mm^2 (n = 40) for sporulating blades. Blades were placed in clean F/2 medium for 24 h before beginning exposures at t = 0.

Exposures selection

Three environmental changes (hyposalinity, marine heatwaves, and WWTPE) were tested. The effluent was collected over a 24-h period from the IVAR Sentralrenseanlegg Nord-Jæren (Mekjarvik, Norway) wastewater treatment plant in January 2025, promptly frozen in aliquots, and thawed before use. The concentration and diffusion rates of the WWTPE were previously modelled, and the 1% WWTPE

concentration (Table 1) in corresponding exposures was chosen based on this data (Pampanin et al. 2024). This plant is the second largest in Norway, serving over 300,000 inhabitants and various industrial activities (IVAR 2018). It operates according to Norwegian regulations, and legacy contaminant concentrations are below legal toxicity thresholds. Further, potential nutrients are removed and sold as activated sludge fertiliser, and the WWTPE therefore primarily presents a real mixture of chemicals, including both legacy and emerging contaminants (Table S1; Pampanin et al. 2024). All three conditions were tested individually, and in all possible combinations, in addition to a control maintained in standard conditions (Table 1; group IDs are used to refer to exposure groups in the manuscript and figures).

Experimental setup

To 250-mL conical flasks containing 200 mL of F/2 medium were added 1 vegetative and 1 sporulating blade, and 5 replicate flasks were used for each group (Table 1, Fig. 1). Control (Ctrl), salinity (Sal), and wastewater treatment plant effluent (WWTP) groups were exposed for 14 days in an incubator (t = 0–2w; Fitotron SGC120, Weiss Technik, Germany). Marine heatwave (MHW) groups were placed in a separate incubator (MLR-352-PE), the temperature was raised by 1 ℃ every 12 h until it reached 10 ℃, then maintained at 10 ℃ for 12 days before decreasing the temperature by 1 ℃ every 12 h until reaching 7 ℃, for a total of 14 days (t = 0–2w). All blades were maintained in 30 µmol photons m^{-2} s^{-1} light, 12h:12h L:D cycle with aeration. Following exposures, all blades were returned to standard conditions and allowed to recover for one week for a total experimental time of three weeks, corresponding to a realistic duration for sporulating thalli. Vegetative blades were maintained for a further five weeks to assess potential recovery in non-reproductive scenarios.

Throughout the experiment the cultivation medium was changed weekly, and the pipettes used for aeration fortnightly. During the initial assignment of blades to exposures (t = 0) and at each medium change, each blade was visually inspected for physiological changes, weighed and photographed for measurement of total increase in surface area (except after 5 weeks of recovery, t = 7w). The photosynthetic ability was also measured weekly (except after 4 and 5 weeks of recovery, t = 6w, 7w); ten random blades (five vegetative, five sporulating) were measured at t = 0, and their values were considered as the baseline for their group.

Table 1 Exposure group information. MHW: marine heatwave; WWTP: wastewater treatment plant effluent (treatment name); WWTPE: wastewater treatment plant effluent

Group ID	Group	Conditions
Ctrl	Control	Standard conditions (32 PSU, 7 ℃)
Sal	Hyposalinity	24 PSU, 7 ℃
MHW	Marine heatwave	32 PSU, 10 ℃
WWTP	WWTPE	32 PSU, 7 ℃, 1% WWTPE
Sal+MHW	Hyposalinity + Marine heatwave	24 PSU, 10 ℃
Sal+WWTP	Hyposalinity + WWTPE	24 PSU, 7 ℃, 1% WWTPE
MHW+WWTP	Marine heatwave + WWTPE	32 PSU, 10 ℃, 1% WWTPE
Sal+MHW+WWTP	Hyposalinity + Marine heatwave + WWTPE	24 PSU, 10 ℃, 1% WWTPE

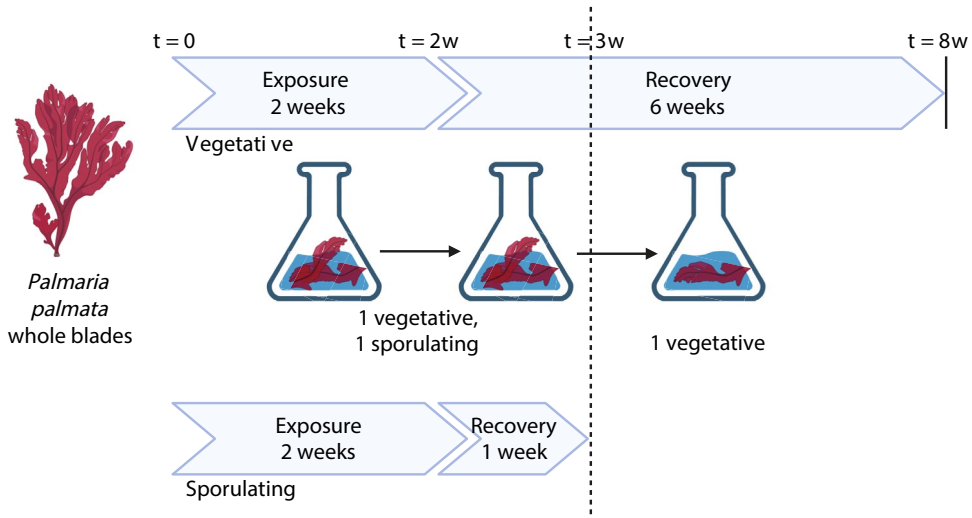


Fig. 1 Experimental timeline, t = time; w = week(s). Created in BioRender

Growth measurements

Growth was measured in both FW and blade surface area (SA). For FW, blades were briefly spun in a salad spinner to remove surface water with minimal stress, then weighed. Blades were then placed flat between two petri dishes and photographed using a Tough TG-6 camera (Olympus, Japan). The total SA of each blade was measured using the ImageJ software (Schneider et al. 2012). In both cases, relative growth rates (RGR) were calculated weekly according to Eq. 1, with X_1 and X_2 the measurements (SA and FW) at times t_1 and t_2 (days), respectively.

$$RGR = \frac{\ln(X_2) - \ln(X_1)}{t_2 - t_1} \times 100 \quad (1)$$

Photosynthetic ability measurements

Blades were dark acclimated for 10 min, after which rapid light curves were obtained using an AquaPen AP-110/P pulse-amplitude modulated (PAM) fluorometer (Flash pulse: 30; super pulse: 70; actinic pulse: 30 µmol photons m^{-2} s^{-1}; Photon Systems Instruments, Czech Republic). The light curves were analysed using the phytotools package in the R Statistical Environment (Silsbe and Makin 2015; R Core Team 2025) to calculate the maximum relative electron transport rate ($rETR_{max}$). The maximum quantum yield of PSII (F_v/F_m) was reported as a measure of potential stress damage to photosystem II, while $rETR_{max}$ was used to assess overall photosynthetic ability.

Statistical testing

Statistical testing was conducted in R. The data did not meet the assumptions of normality and homoscedasticity for parametric testing. For all repeated measurements (SA, FW, F_v/F_m, and $rETR_{max}$), the longitudinal data were assessed using a non-parametric, rank-based repeated measure test (function f1.ld.f1 in package nparLD, Noguchi et al. 2012), testing the group (exposure × reproductive stage) × time interaction during the first three weeks of experiment, and the exposure × time interaction in long-term recovery testing in vegetative samples. Pairwise comparisons generated by this function were Holm-adjusted. Nonparametric Dunnett's tests were also performed at individual timepoints to compare each exposure with controls (nparcomp package, Konietschke et al. 2015). The growth curves (SA and FW, absolute values) of vegetative blades after long-term recovery were fitted to both linear and exponential models, and the best fit was assessed using Akaike information criteria (AIC). Absolute size measurements (SA and FW) were also tested using a one-way ANOVA (factor: exposure) at the final time point for sporulating (t = 3w) and vegetative (t = 8w) blades to assess overall potential effects on growth. For all tests, differences were considered significant for $p < 0.05$. All results are reported as mean ± standard error ($n = 5$).

Results

Growth

During the first three weeks of the experiment, there was a significant effect of the exposure × time interaction on both SA and FW RGRs (Table S2). In vegetative blades, SA growth rates of control blades (1.65 ± 0.32 % day^{-1}; Fig. 2A, C) were significantly lower than those exposed to Sal (2.22 ± 0.37 % day^{-1}), MHW (2.37 ± 0.39 % day^{-1}), and Sal+MHW (2.78 ± 0.36 % day^{-1}). Dunnett's tests showed all these exposures led to significantly higher SA RGRs than controls during the second week of the experiment.

In sporulating samples, SA growth was highest in blades exposed to Sal+WWTP+MHW (2.13 ± 0.15 % day^{-1}; Fig. 3A, C), significantly higher than controls (1.17 ± 0.43 % day^{-1}) and blades exposed to Sal (0.97 ± 0.39 % day^{-1}), Sal+WWTP (0.89 ± 0.57 % day^{-1}), and Sal+MHW (1.91 ± 0.23 % day^{-1}). Despite no other longitudinal differences, during the second week, all exposures except Sal and Sal+WWTP led to significantly higher SA RGRs than controls. Only blades exposed to Sal were different between reproductive stages, with vegetative blades growing significantly faster (2.22 ± 0.37 % day^{-1}) than sporulating ones (0.97 ± 0.39 % day^{-1}).

Growth rates were generally higher in FW (average 3.09 ± 0.35 % day^{-1}; Fig. 2B, D; Fig. 3 B, D) than in SA (average 1.84 ± 0.32 % day^{-1}). In vegetative blades, the decrease in control growth during week 2 was not observed, and no exposure led to a significant difference with controls over time. Sporulating blades were characterised by differences in trajectories leading to numerous significant differences. Both control blades and those exposed to Sal+WWTP+MHW had average RGRs during exposures which increased dramatically during the recovery week and were significantly different from all other exposures except each other. Vegetative blades exposed to Sal+WWTP+MHW had significantly higher RGRs (4.53 ± 0.59 % day^{-1}) than sporulating ones (2.82 ± 0.27 % day^{-1}). Blades exposed to Sal+MHW also had significantly different FW growth depending on reproductive stage, although this was primarily driven by trajectory (Fig. 2D, 3D).

After one week of recovery, sporulating blades averaged 3592 ± 232 mm^2 and 1311 ± 75 mg in SA and FW, respectively (Fig. S1). The blades varied significantly between treatments, both in SA ($F(7, 32) = 4.40$, $p = 0.002$) and FW

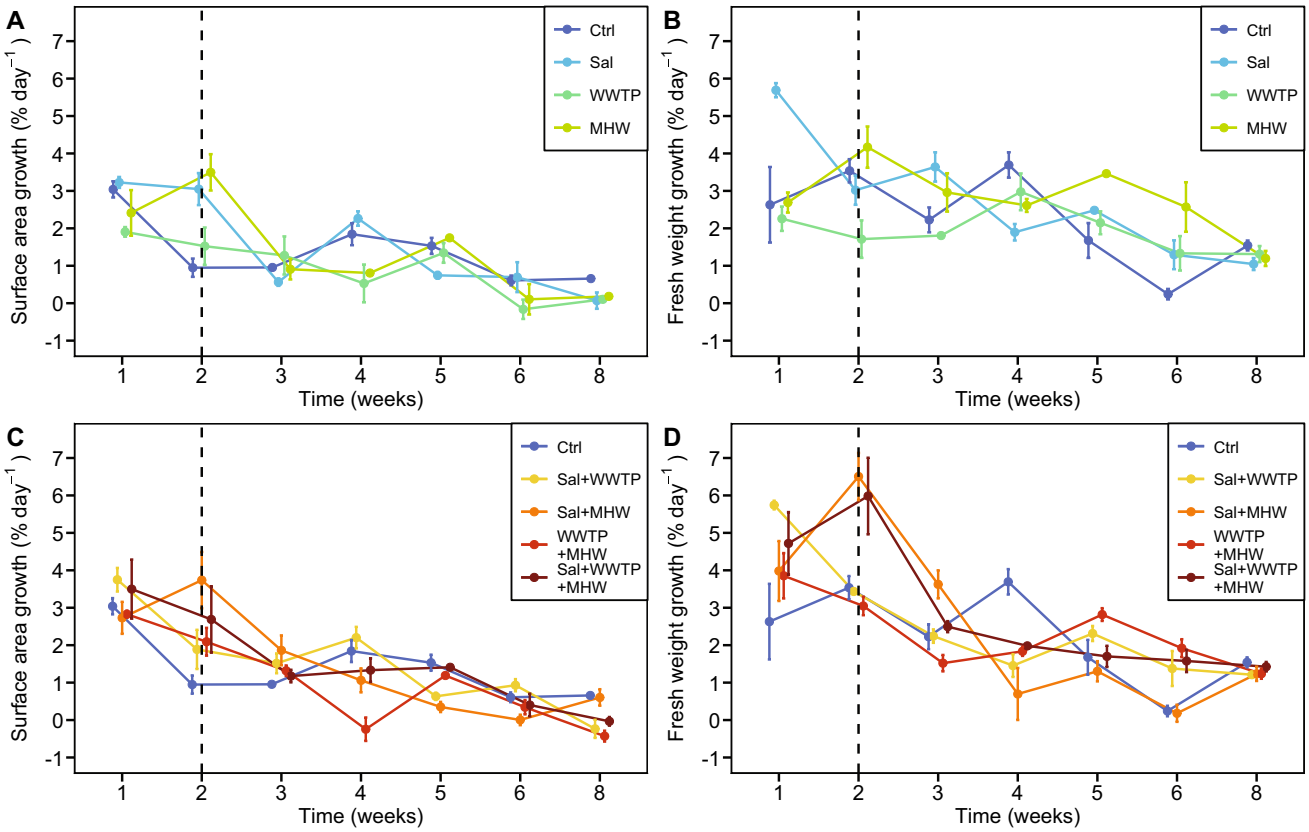


Fig. 2 Daily relative growth rates in surface area (**A**, **C**) and fresh weight (**B**, **D**) of vegetative blades of *Palmaria palmata* exposed to single (**A**, **B**) and combinations of (**C**, **D**) anthropogenic environmental changes for two weeks (left of the dashed lines), followed by five weeks of recovery. Data reported as mean value points with standard errors (n = 5). Ctrl: control, Sal: hyposalinity, WWTP: wastewater treatment plant effluent, MHW: marine heatwave

(F(7, 32) = 4.09, p = 0.003). For both measurements, Sal (2464 ± 115 mm^2, 956 ± 66 mg) and Sal+WWTP (2527 ± 145 mm^2, 951 ± 67 mg) led to significantly smaller blades than WWTP (5242 ± 422 mm^2, 1758 ± 163 mg) and MHW (4977 ± 839 mm^2, 1834 ± 229 mg). Blades exposed to WWTP had significantly higher SA than controls (2777 ± 473 mm^2), and those exposed to MHW had significantly higher FW than controls (1017 ± 165 mg).

Vegetative blades allowed to recover for five weeks after exposures all showed a similar decrease in growth rates for both SA and FW, with respective average RGRs of 0.11 ± 0.08 and 1.29 ± 0.08 % day^{-1} during the last two weeks of the experiment (Fig. 2). Nonetheless, significant differences in the longitudinal data remained, driven largely by different trajectories (Table S3). Notably, blades exposed to Sal and Sal+WWTP had significantly different FW RGRs than controls, while those exposed to Sal, MHW, Sal+MHW, and WWTP+MHW all had significantly different SA RGRs than controls. During the last two weeks, Dunnett's tests showed no effects of exposures on the FW RGRs, while blades previously exposed to Sal, WWTP, MHW, WWTP+MHW, and Sal+WWTP+MHW all had lower SA RGRs than control blades. Nonetheless, AIC measures showed that absolute measurements of FW and SA followed exponential curves for all exposures and controls, and the blades reached an average SA of 4092 ± 184 mm^2 and FW of 2003 ± 107 mg by the end of the experiment (Fig. S2). There were no significant differences in either SA (F(7, 32) = 0.192, p = 0.985) or FW (F(7, 32) = 1.55, p = 0.186) between exposures at the end of the experiment.

Photosynthetic efficiency

The group × time interaction significantly affected both measures of photosynthetic efficiency during the first three weeks of the experiment (Table S4). According to the repeated measures test, the longitudinal trajectory of maximum quantum yields of PSII (F_v/F_m) showed no differences between reproductive stages for any exposure (Fig. 4A, C and 5A, C). In vegetative blades, exposure to both MHW and WWTP+MHW led to significantly lower overall F_v/F_m (0.33 ± 0.02 and 0.30 ± 0.02, resp.) than control blades (0.47 ± 0.02). Sal-treated blades also had a significantly different trajectory in their F_v/F_m measurements but had

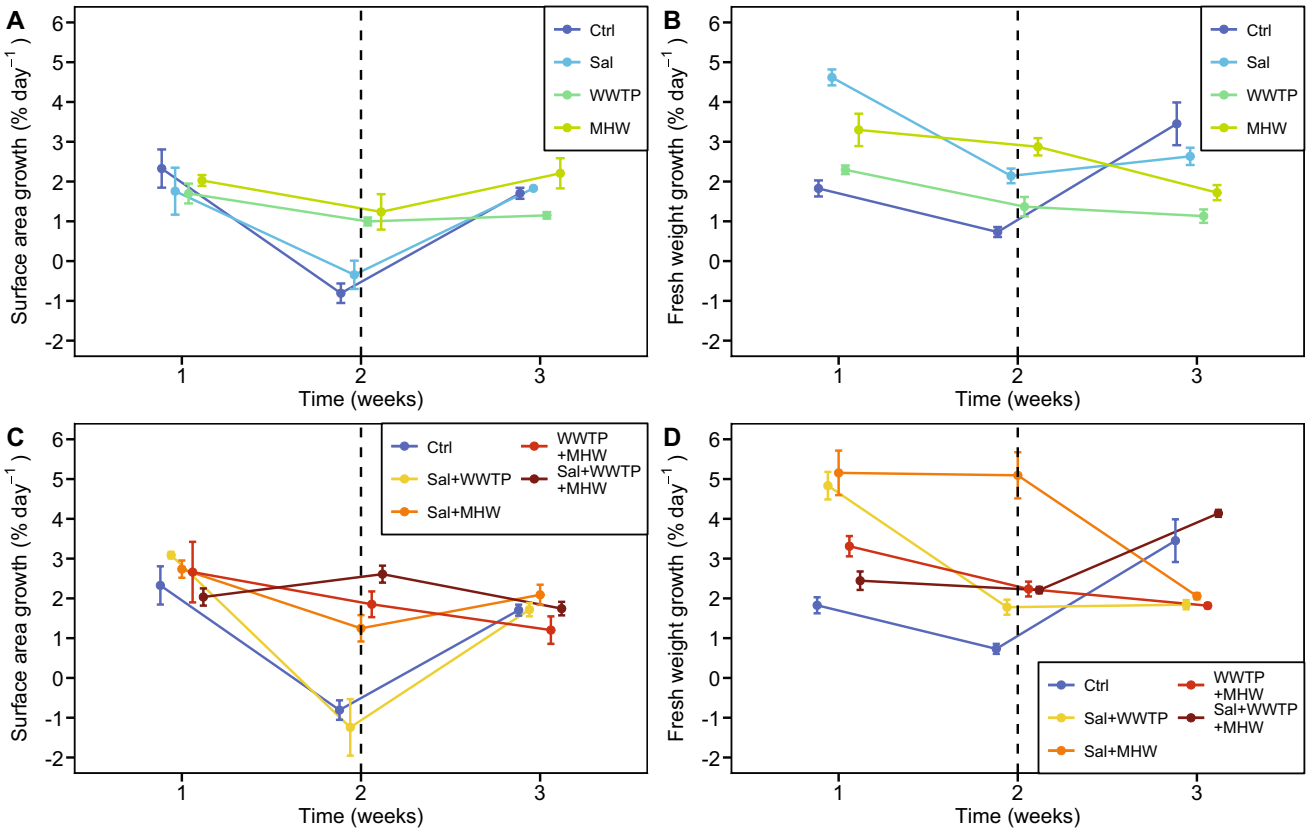


Fig. 3 Daily relative growth rates in surface area (**A**, **C**) and fresh weight (**B**, **D**) of sporulating blades of *Palmaria palmata* exposed to single (**A**, **B**) and combinations of (**C**, **D**) anthropogenic environmental changes for two weeks (left of the dashed lines), followed by one week of recovery. Data reported as mean value points with standard errors (n = 5). Ctrl: control, Sal: hyposalinity, WWTP: wastewater treatment plant effluent, MHW: marine heatwave

similar average values (0.43 ± 0.01). None of the exposures changed the F_v/F_m trajectories of sporulating blades compared to controls.

On the other hand, many differences were observed at individual time points. After one week, all exposures led to significantly lower F_v/F_m than controls in vegetative blades (Fig. 4A, C). Blades exposed to MHW, Sal+MHW, and WWTP+MHW also had significantly lower F_v/F_m at two and three weeks, while those exposed to WWTP and Sal+WWTP+MHW showed no difference after two weeks but had again lower values after three weeks. Sporulating blades exposed to MHW, Sal+WWTP, Sal+MHW, and WWTP+MHW all had significantly lower F_v/F_m than controls at all three time points (Fig. 5A, C). Blades exposed to Sal had significantly lower F_v/F_m than controls after one week, but not at other time points.

The $rETR_{max}$ showed significantly different trajectories in blades exposed to Sal in vegetative (21.6 ± 1.9) and sporulating blades (43.8 ± 5.4), while other exposures did not produce different results across reproductive stages (Fig. 4B, D and 5B, D). Sal also led to significantly lower $rETR_{max}$ than controls (33.7 ± 0.9) in vegetative blades. Otherwise, there were no significant differences between trajectories of exposures and controls for either vegetative or reproductive blades. In sporulating blades, individual time points also showed few differences, with only blades exposed to Sal and Sal+MHW having significantly lower values than controls after one week (Fig. 5B, D). In vegetative blades, however, Sal, Sal+MHW, WWTP+MHW, and Sal+WWTP+MHW all led to significantly lower $rETR_{max}$ than controls at all three time points, while Sal+WWTP produced lower values after one week, and WWTP and MHW after two weeks (Fig. 4B, D).

Longer recovery times of vegetative blades still produced several measurable differences in F_v/F_m (Fig. 4A, C; Table S5). Seaweeds exposed to WWTP (0.38 ± 0.01 average), MHW (0.32 ± 0.01), Sal+WWTP (0.40 ± 0.01), Sal+MHW (0.33 ± 0.01), and WWTP+MHW (0.32 ± 0.01) all had different trajectories than controls (0.43 ± 0.01). After four and five weeks, WWTP, MHW, and Sal+MHW led to significantly lower F_v/F_m than Ctrl, while WWTP+MHW values were lower at all time points. At the end of the experiment, only blades exposed to WWTP+MHW had lower values than controls.

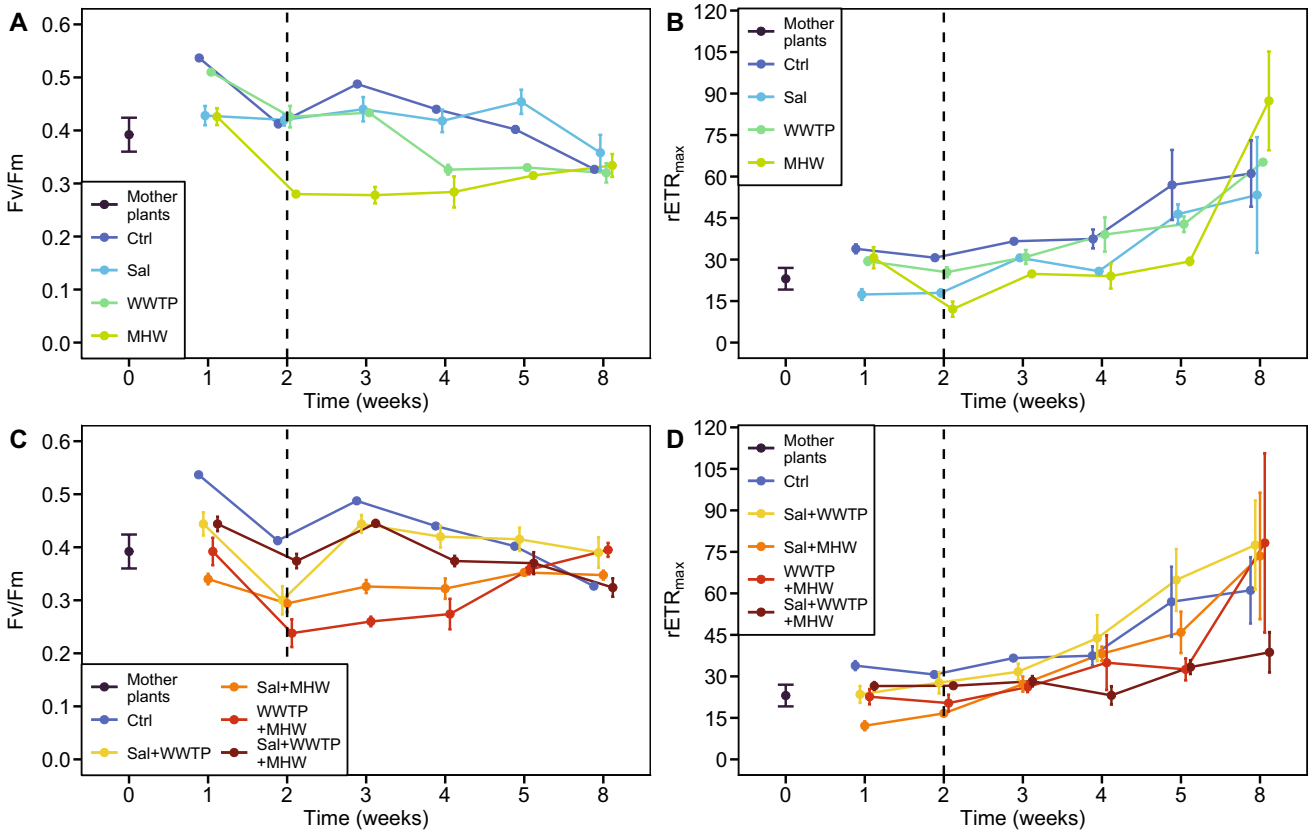


Fig. 4 Photosynthetic parameters of vegetative blades of *Palmaria palmata* exposed to single (**A**, **B**) and combinations of (**C**, **D**) anthropogenic environmental changes for two weeks (left of the dashed lines), followed by five weeks of recovery. A, C: Maximum quantum yield of PSII; B, D: Maximum relative electron transport rate ($rETR_{max}$). Data reported as mean value points with standard errors ($n = 5$). Ctrl: control, Sal: hyposalinity, WWTP: wastewater treatment plant effluent, MHW: marine heatwave

Fewer differences were recorded in $rETR_{max}$ values after longer recovery. Only blades treated with Sal (30.4 ± 3.6) and Sal+MHW (33.5 ± 4.5) differed from Ctrl blades (42.8 ± 3.6) overall, with Sal also producing lower $rETR_{max}$ after four weeks.

DISCUSSION

Exposure effects were mild and transient

This flask-based experiment investigated potential effects of climate- and pollution-related environmental change in individual blades of *P. palmata*. Both growth measurements showed no decreases in response to exposures, while several conditions instead led to temporarily increased growth in *P. palmata* blades. The lack of differences in the overall growth patterns and final size of vegetative samples after six weeks of recovery suggests that the exposure effects recorded during the first three weeks of the experiment were transient and lacked long-term consequences on the health and physiology of the blades. This is further supported by the exponential growth observed for all groups, characteristic of healthy growth patterns in seaweeds (Yong et al. 2013). Additionally, while several exposures initially decreased the F_v/F_m of blades, the total electron transport rates were largely unaffected by treatments, and the F_v/F_m recovered in vegetative blades after six weeks post-exposure. These results challenge the hypothesis that the tested conditions would negatively affect the blades. The exposures selected as anthropogenic environmental changes may instead have been more favourable to growth, with minimal adverse effects. While growth in *P. palmata* is generally limited in the winter, it is highest in spring/summer, where combinations of higher temperatures, increased irradiance, and nutrient availability provide optimal conditions (Stévant et al. 2023). Previous studies found no decrease in growth rates at temperatures below 15 ℃ (Semmouri et al. 2025) and 17 ℃ (Corey et al. 2012), although in populations located at lower latitudes. The MHW exposures may therefore have improved conditions for growth, with heating sufficiently gradual and limited to avoid causing damage.

Seaweeds are also generally resilient to salinity decreases, especially intertidal species such as *P. palmata*. Two

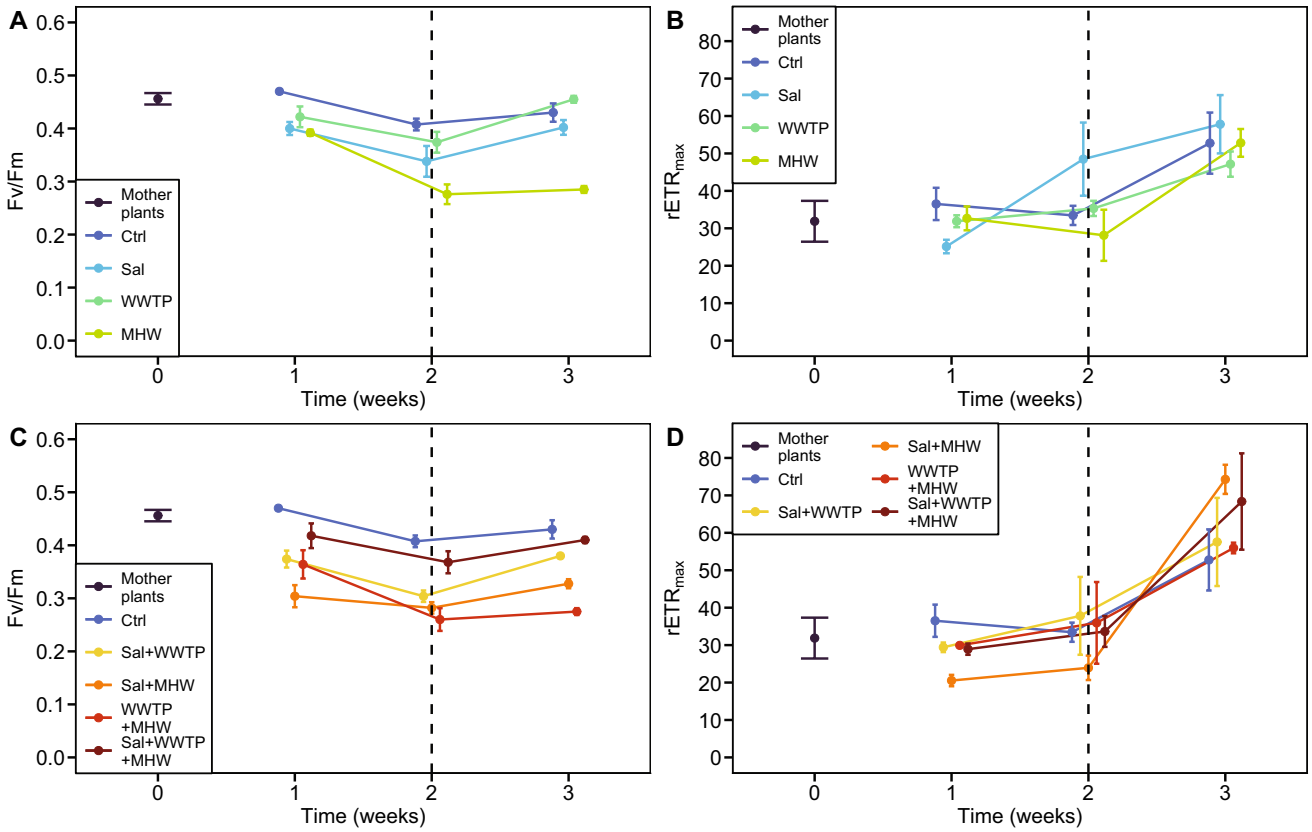


Fig. 5 Photosynthetic parameters of sporulating blades of *Palmaria palmata* exposed to single (**A**, **B**) and combinations of (**C**, **D**) anthropogenic environmental changes for two weeks (left of the dashed lines), followed by one week of recovery. A, C: Maximum quantum yield of PSII; B, D: Maximum relative electron transport rate (rETR$_{max}$). Data reported as mean value points with standard errors ($n = 5$). Ctrl: control, Sal: hyposalinity, WWTP: wastewater treatment plant effluent, MHW: marine heatwave

studies assessing the effects of 15 PSU salinity on *P. palmata* reported contrasting results: thalli from Spitsbergen had high photoinhibition and mortality within four days of exposure (Karsten et al. 2003), while Danish fronds had the highest growth rates at this salinity (Schmedes and Nielsen 2020). Population differences may therefore strongly affect the observed response. In the present study, the sampling site is located between the mouths of two fjords, and local populations may be adapted to regular decreases in salinity. Similarly, in the chlorophyte *Ulva prolifera*, hyposaline conditions (20 PSU) increased growth compared to standard (30 PSU) in a Chinese strain, but not in a Korean one (Bao et al. 2023). Physiological stress often arises in harsher hyposaline conditions or after longer exposures, which may not be as environmentally relevant (Daglio et al. 2022; Siddiqui et al. 2022).

Effects of complex pollutant mixtures are rarely studied. Exposure to WWTPE may also have had toxic effects on competing microorganisms, such as bacteria and epiphytes, thus improving general conditions for the growth of *P. palmata* blades. However, the effects observed were small, and the removal of known pollutants and excess nutrients from the effluent appears successful in limiting effects on ecosystems. Norwegian wastewater treatment regulations align with EU frameworks, and the WWTPE effects observed are likely to be similar to those in plants serving medium-sized European cities. However, the WWTPE collected corresponds to a single 24-hour period, and both pollutant composition and concentrations are expected to vary over time. Spatiotemporal differences in cultural and industrial practices are also expected to affect influent composition and, in turn, effluent characteristics, especially for emerging pollutants. Such variations may affect the outcomes for wild populations.

In photosynthetic measurements, the overall stability and moderate decrease observed in F_v/F_m throughout the eight weeks of experiment contrasts with the long-term increases recorded in rETR$_{max}$. These increases were primarily observed during the recovery phase, including in controls, suggesting an effect of the lab-based conditions rather than the exposures. F_v/F_m represents the maximum quantum yield of PSII, and is therefore near maximum in healthy seaweeds, with little effect of increased nutrient availability. On the other hand, more proteins and pigments involved in

photosynthetic processes may be synthesised in response to nutrient excess, leading to an overall improvement of electron transport rates (Martins et al. 2023). The increase in nutrient availability, therefore, appears to affect the photosynthetic ability in *P. palmata* more than any potential stress caused by the exposures. The complete lack of significant differences with controls at the last time point further suggests an absence of long-term damage by the exposures and highlights the resilience of *P. palmata* to realistic pollution and sudden changes in environmental conditions. Nonetheless, the exposures tested in this study present a large and abrupt departure from standard conditions, and some degree of adaptive mechanisms is likely to have led to the stress resilience observed.

Exposures as stressors and possible adaptation

Despite the lack of adverse effects on growth, F_v/F_m results demonstrated that the exposures produced stress effects. This was effectively prominent during the first week of exposures, where all but two groups had lower F_v/F_m than controls, indicating a sharp adverse effect of the tested conditions. Such decreases were also observed after a week of recovery, suggesting potential functional damage rather than a temporary downregulation of related processes. While such damage was not consistently reflected in overall electron transport rates, transient decreases in $rETR_{max}$ after exposure to Sal, MHW, and several combined exposures still appeared to indicate some deterioration of overall photosynthetic efficiency, especially in vegetative blades. While exposures significantly decreased the maximum efficiency of PSII, effects on the overall electron transport rate were minimal. This may indicate that adaptation mechanisms exist in *P. palmata* to compensate for decreased PSII efficiency without compromising the entire electron transport chain. Indeed, chronic PSII inhibition in seagrasses can be compensated by increases in non-photochemical quenching (NPQ) and cyclic electron transport driven by PSI, maintaining ETR_{max} and consistent overall photosynthetic efficiency (Fang et al. 2020). Similar effects have also been reported in the brown seaweed *Fucus serratus* under thermal stress. While the F_v/F_m measurements were related to health and survival, ETR was instead correlated to growth rates (Figueroa et al. 2019). The consistency in growth rates and $rETR_{max}$ in this study appears to indicate similar trends. Longer stress exposures have been shown to reduce these compensation mechanisms, as have stronger stressors (Liang et al. 2022).

In land plants, stress often triggers a defence-growth trade-off, which has also been commonly observed in seaweeds, including in *P. palmata* (Zhang et al. 2020; Liboureau and Pampanin 2024). However, in this study, growth was mostly increased by exposures, albeit temporarily. Hormesis, a positive metabolic response to low-level stress, is well documented in vascular plants, often leading to increased growth (Agathokleous et al. 2019; Yuan et al. 2019). Despite its prevalence, it is yet to be documented in seaweeds, with most research focusing on highly stressful or sublethal conditions.

Further studies are needed to elucidate the molecular response and identify the specific mechanisms of adaptation leading to stable growth and photosynthetic rates in *P. palmata* under varying environmental conditions.

Exposure combinations were not synergetic

All three single exposures produced generally similar effects, with limited, transient adverse effects on photosynthetic measurements contrasting with moderate increases in growth. Nonetheless, these effects varied between exposures, indicating unique responses to each stimulus rather than a generic response from the *P. palmata* blades. MHW, both as a single exposure and combined with others, appeared to cause decreases in F_v/F_m most consistently. Heat stress has been recorded to decrease the photosynthetic efficiency in several rhodophyte species, although this was usually associated with reduced growth (Urrea-Victoria and Chow 2024; Zhao et al. 2025). On the other hand, the general seaweed tolerance to hyposaline conditions was observed in both growth and photosynthetic measurements (Shindo et al. 2022).

Combined conditions were also complex. There was no indication of synergistic effects, with multi-exposures yielding responses similar to those of one of their individual components. However, the dominance of individual exposures was unclear and appeared to change for each parameter, with Sal and MHW appearing to drive the responses in growth measurements. In contrast, WWTP and MHW seemed to have an increased effect on photosynthetic efficiency. Some combinations may be antagonistic; Sal appeared to decrease the impact of WWTP on growth, while the triple combination Sal+WWTP+MHW had fewer overall differences with controls (13 across all statistical tests) than double combinations (Sal+WWTP: 15; Sal+MHW: 20; WWTP+MHW: 18). In the green seaweed *Ulva prolifera*, higher temperatures and nutrient abundance increased the hyposalinity tolerance, showing similar antagonist effects between exposures (Bao et al. 2023). The mechanisms by which individual and combined conditions affect the physiology of *P. palmata* remain to be elucidated.

Differences between reproductive stages were limited

Seaweeds tend to allocate more resources to growth when vegetative, with energy focused on meiosis and spore formation in sporulating specimens (Liu et al. 2017). In the

rhodophyte *Gracilaria chilensis*, which presents a similar haplodiplontic life cycle as *P. palmata*, reproductive fronds show consistently lower growth rates and photosynthetic efficiency than vegetative ones (Guillemin et al. 2014). While higher growth was indeed observed in blades exposed to Sal, Sal+MHW, and Sal+WWTP+MHW, other conditions did not result in different growth between reproductive stages. Overall, this study's results contradict the hypothesis that sporulating blades would be more vulnerable to anthropogenic environmental changes than vegetative ones. The growth of sporulating blades was instead increased more consistently by exposures than that of vegetative ones, and they were also generally more resilient to damage to photosynthetic processes. In some species, gametophytes require specific conditions to develop and reproduce, and abrupt changes to environmental conditions can disrupt sporulation in sporophytes (Martins et al. 2022; Korabik et al. 2023). While this has not been described in *P. palmata*, these results may indicate a change in the normal reproductive metabolism, with potential impacts on subsequent reproduction. On the other hand, the increased resilience of sporulating blades may point to increased resource investment into producing and releasing spores, which are often more resistant to harsh climate conditions than sporophytes (Silva et al. 2022). Stress-induced reproduction is documented in several rhodophyte species (Suda and Mikami 2020), although further physiological and molecular studies are needed to assess these hypotheses. Further studies evaluating the potential effects of exposures on spore release, recruitment, and F1 success would help document both potential damage to sporulation processes and transgenerational priming effects.

Practical outcomes for conservation and cultivation

The results of this study highlighted the resilience of *P. palmata* to environmental changes likely to affect the species in the coming decades. None of the evaluated exposures appear to cause significant medium- or long-term damage, despite representing the limits of currently expected extreme weather events or widespread pollution for this population. It is possible that, despite mild stress, hormesis allowed the blades to withstand the exposures. Such mechanisms are a key element of adaptive plasticity in vascular plants, and can also play a role in plastic memory, leading to improved response to later occurrences of similar stress (Erofeeva 2022). These effects are commonly used in crops, where priming seeds or even parental plants with mild stress conditions can help improve seedling response to common environmental stressors (Cooper and Ton 2022; Liu et al. 2022). Similar work using epigenetic memory to prime kelp seedlings has been attempted and could help protect both cultivated and reforested seaweed populations, although the duration of this epigenetic memory remains to be elucidated (Gauci et al. 2024). In wild populations, the forecasted increase in frequency of sudden changes in conditions may help both maintain a plastic memory and select more resilient individuals. Nonetheless, the biology and physiology of *P. palmata* vary widely across seasons and reproductive stages, and further investigations may reveal some vulnerabilities of populations to arising challenges. Marine heatwaves during summer months are more likely to raise temperatures near lethal conditions, and high-stress events during a key period for seaweed growth may lead to population-wide consequences. This experiment was also conducted on a small scale, assessing individual blade responses in semi-static, flask-based conditions. Such a setup enabled precise control of experimental conditions and direct assessment of exposure effects on individual thalli physiology, increasing the reliability of the results. On the other hand, it may not accurately reflect changes in conditions in either wild populations or cultivation facilities with water flow-through, and larger-scale studies will further inform the practical outcomes of this research.

Conclusion

Short exposures to single and combined realistic anthropogenic environmental changes had little overall effect on vegetative and sporulating blades of *P. palmata*. Some moderate, transient decreases in photosynthetic efficiency were observed during exposures and early recovery, but no differences were noted by the end of the eight-week experiment. All tested exposures (marine heatwaves, hyposalinity, and wastewater treatment plant effluent) had unique effects on the growth and photosynthetic efficiency of the seaweed, and no synergetic effects were noted in the multi-stressor exposures, with some indications of antagonism, especially when combining all three exposures. The increased growth displayed by sporulating blades may indicate a shift in metabolic priorities in response to the exposures. Decreased resource allocation to sporulation could lead to reduced reproductive output, with potential long-term consequences for populations, which warrants further investigation. On the other hand, the general resilience of vegetative blades appears to be positive for the future of wild populations, and such hormesis could potentially be used in cultivation to develop priming methods and improve the reliability of the industry. Mechanistic investigations identifying the specific nature and duration of molecular changes would be crucial to understand whether exposures trigger a stress response or simply provide better conditions for growth, and how they might affect *P. palmata* populations in long-term or repeated exposures.

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Authors' contributions PL conceptualised and conducted the experiments, analysed the data, prepared the figures and wrote the manuscript. RMO conceptualised and conducted the experiments and revised the manuscript. LMSG conceptualised the experiments, revised the manuscript, and supervised RMO. DMP conceptualised the experiment, revised the manuscript, supervised PL and RMO, and acquired funding. All authors have read and approved the final manuscript.

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Data availability All data generated for this study, and the code used to analyse the data, are uploaded to Mendeley Data and available through this link: doi.org/https://doi.org/10.17632/mn3g5c5zdf.3.

Declarations

Competing interests The authors declare no competing interests.

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