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Hyposalinity affects diurnal photoacclimation patterns in the rhodophyte *Palmaria palmata* under mimicked Arctic summer conditions

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ABSTRACT

Ocean temperatures have increased during 2011–2020, causing significant changes in the marine environment. One area that has been affected by the temperature increase is the Arctic, leading to a decrease in glacial mass and an increase in meltwater. Some organisms *e.g., Fucus* (brown seaweed) benefit from these environmental changes while others may be strongly affected. *Palmaria palmata* (Rhodophyta), an alga that inhabits the arctic, intertidal and upper subtidal zones, is directly influenced by variations in the daily cycles of irradiance and temperature and being affected by low salinities. Fronds of *P. palmata* were collected during the summer of 2019, in Kongsfjorden, Svalbard (78.9°N, 11.9°E). For 21 days at 0 °C, the material was subjected to variations in daily irradiance cycles reaching minimum values of 50 μmol photons m^{-2} s^{-1} and maximum values of 500 μmol photons m^{-2} s^{-1}. These conditions were complemented with three different salinities S_A 34 (control), 28, and 18. Subsequently, measurements of photosynthetic parameters such as F_v/F_m, NPQ, biochemical parameters such as pigment quantification (Chl *a*, Lut, Zeax, β-Car, PE, PC, APC), and antioxidant activity (DPPH) were carried out. In general, for *P. palmata*, salinity was the factor that negatively affected photosynthetic activity, with F_v/F_m showing a decrease in values towards the end of the experiment with S_A 28 and 18. With S_A 34, *P. palmata* can respond more effectively to variations in daily irradiance, whereas, as salinity decreases, its response capacity is diminished. These data are supported by variations in the daily pigment concentration of Chl *a*, β-Car, and Zeax, the latter occurring at low concentrations, showing variations in daily irradiance cycles at S_A 28 and 18. Phycobilins, in general were found to be more sensitive to irradiance variations, while antioxidant activity - DPPH, was influenced by both daily irradiance cycles and low salinity. The physiological response of *Palmaria palmata* shows its tolerance to daily irradiance variation, which is restricted by decreasing salinity. This kind of acclimation to different factors may generate a high energy expenditure, which could be reflected in the growth rate of the species in the Arctic, leading to a decline of Arctic populations in the future.

1. Introduction

Ocean temperature has increased during the period 2011–2020 by (0.88 [0.68 to 1.01] °C) compared to the period 1850–1900 [1], with the potential of causing significant changes in the marine environment. The area most significantly affected by temperature increase in recent decades is the Arctic [2] and Arctic fjords are regarded as particularly important in climate regulation, serving as an interface between sea and land [3]. The Arctic region of Svalbard has attained particular interest in recent decades, as it is strongly hit by temperature increase, promoting glacial retreat and meltwater runoff [4–6]. The surface waters of Svalbard fjords are usually characterized by a freshwater layer from glacier melt, river runoff, and ablation [7]. This situation is most pronounced towards the summer. Another characteristic is that this hyposaline

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surface layer is thicker towards the inner part of the fjord than towards the mouth of the fjord and, hence, is related to a spatial gradient of fjord temperature and salinity [3]. These characteristics directly affect the organisms that inhabit the intertidal and shallow subtidal zones.

In recent years, it has been observed that some algae did indeed benefit from environmental variations in Svalbard, in example with an increase in biomass and occurrence of kelps and algae of the genus *Fucus* [8]. In general, algae can acclimate to changes in environmental factors, *e.g.,* temperature, irradiance, salinity [9–11]; however, this process usually comes along with metabolic trade-offs. As an example, photosynthetic quantum yield F_v/F_m is directly affected under variations of environmental parameters in Arctic algae: at temperatures above 15 °C, the Arctic endemic kelp *Laminaria solidungula* is not able to compensate osmotic strain, which is reflected by decreasing F_v/F_m [10]. Also, under hyposalinity conditions, the kelp *Saccharina latissima* shows a decrease in F_v/F_m and growth rate [12]. However, irrespective of any other environmental variation algae must also regulate their photosynthetic performance in a diurnal pattern, based on the irradiance variations occurring in the course of the day, even under high Arctic summer conditions [13, 14]. Usually, in the morning, an increase in photosynthetic activity is observed until maximal capacity is reached, while at midday photoinhibition may occur, followed by recovery in the afternoon, and in the evening, recovery is almost completed [15]. In general, both the daily variations and changes in environmental parameters interact in determining algal performance in the field [14,16,17].

In this respect, the red algal species *Palmaria palmata* (Linnaeus) F. Weber & D. Mohr is of great interest due to its wide distribution range in the North Atlantic, including the Arctic zone [18, 19], being able to inhabit low salinity areas, such as the Fornæs area, Baltic Sea, where salinity ranges from S_A 27.5 - 15 [20]. It is widely used in the food industry, aquaculture, cosmetics, amongst others [17, 21]. The acclimation capacity of *P. palmata* under environmental variation has been well studied: Sagert and Schubert [22] describe how this species, under different light qualities, can modify the concentration of red algal light harvesting and photoprotective pigments phycoerythrin (PE) and zeaxanthin, increasing their concentration under the influence of green light. Field studies on *P. palmata* show how it is able to alter its concentration in β-carotene, lutein, and mycosporine-like amino acids (MAAs) with seasonal variations [16, 23, 24], while laboratory studies showed high temperature-dependence of photosynthetic quantum yield in *P. palmata* from the Arctic [11]. Karsten et al. [25] described acclimation responses under the interaction of UV radiation and salinity variation for *P. palmata*, showing that after 96 h at S_A 15, quantum yield decreased, and samples were bleached by the end of the experiment.

In this study, we have investigated how the red alga *Palmaria palmata*, collected from Kongsfjorden, Svalbard, regulates is ecophysiologal performance along the daily variations in irradiance levels during high Arctic summer conditions and how these processes are modulated by hyposaline conditions. By this we simulated a typical situation occurring in Arctic fjords during the Polar day and challenging benthic organisms in the shallow subtidal. We hypothesize, that daily photosynthetic regulation of *Palmaria palmata* may be negatively affected by exposure to low salinities.

2. Material and methods

2.1. Collection site and algal material

The experiment was conducted at Kings Bay Marine Laboratory, Ny Alesund, Kongsfjorden, Spitsbergen-Svalbard (78.9° N, 11.9° E) during July 2019. Specimens of the red macroalga *Palmaria palmata* were collected in the shallow subtidal zone in front of the Marine Laboratory (78°55′39.8″N; 169 11°55′48.3″E), between 0 - 1 m of depth below low tide level. Samples were cleaned and experimental material was cut from the mid-apical zone of vegetative gametophytic fronds.

2.2. Experimental design and set-up

To evaluate the effects of the low light / high light cycle, as typically occurring during Polar day conditions, and different salinities (S_A) on *P. palmata*, the samples were maintained in a "Pre-control treatment" for 5 days: Samples were kept in seawater (S_A 34), in aerated 1-L tanks and enriched with PES-Provasoli (Fig. 1). The medium was renewed every four days. The samples were kept under constant illumination of 50 μmol photons m^{-2} s^{-1} at 0°C. After this acclimation time, part of the samples was kept at a salinity S_A 34 (used as control), while the other samples were placed at S_A 28 and 18. Low salinities were obtained by diluting the seawater with fresh water and correspond to salinities measured in fjord surface waters close to glacial meltwater zones [26–28].

Specimens subjected to the different salinity treatments were exposed to a light cycle mimicking Polar Day conditions at the study site, ranging from midnight – low light intensity, 50 μmol photons m^{-2} s^{-1} (LL), to midday – high light intensity 500 μmol photons m^{-2} s^{-1} (HL). These cycles were continued for 21 days and applied by gradually increasing or decreasing illumination hour by hour, reaching the lowest (LL) and highest (HL) points every 12 h, using a ProfiLux 3 (with LED Mitras daylight 150, GHL Advanced Technology, Kaiserslautern, Germany) system (Fig. 1). The light intensity values were based on the daily cycle observed by Bartsch et al. [29] in the fjord, who describe midday irradiance values of 350–600 μmol photons m^{-2} s^{-1} between 1.7 and 4.2 m depth (values taken over the seaweed canopy) and midnight values below 100 μmol photons m^{-2} s^{-1}.

A total of 9 beakers of 800 ml ($n = 3$ beakers at S_A 34, $n = 3$ beakers at S_A 28 and $n = 3$ beakers at S_A 18) were used. In each beaker 12 algal tissue samples were kept (6 samples were measured during the HL and 6 samples during LL cycle). This number of samples corresponds to the six measurements taken during the 21 days of culture (days: 1, 3, 6, 10, 15 and 21).

After each photosynthetic measurement, the samples measured were shock-frozen with liquid N_2 and stored at −80 °C. Subsequently, the samples were freeze – dried for 24 h, in order to carry out all the biochemical analysis. Consequently, all analytical values are expressed in relation to dry weight (DW).

2.3. Photosynthetic performance

Photosynthetic parameters corresponding to chlorophyll fluorescence at photosystem II (PSII) were measured using an amplitude-modulated chlorophyll fluorometer (Imaging PAM, Walz GmbH Mess- und Regeltechnik, Effeltrich). After 10 min of dark adaptation, the optimal quantum yield of photosystem II (F_v/F_m) was measured *in vivo*. Subsequently, the photosynthesis – irradiance (P-E) curve was measured *in vivo*, recording ten steps of increasing irradiance. With these data, the non-photochemical quenching (NPQ) was obtained according to Serôdio and Lavaud [30] and reflecting the photoprotective capacity of the photosynthetic apparatus.

2.4. Pigment analysis

Lyophilized samples ($n = 3$) were used in pigment analysis using a high-performance liquid chromatography LaChromeElite® system equipped with a chilled autosampler L-2200 and a DAD detector L-2450 (VWR- Hitachi International GMBh, Darmstadt, Germany), according to the method described by Koch et al. [31] modified for red algae. Separation of pigments was performed according to Wright et al. [32]. The following photosynthetic and accessory pigments were extracted and quantified by HPLC: Chlorophyll *a* (Chl *a*), β-Carotene (β - Car), Zeaxanthin (Zeax), and Lutein (Lut).

Phycobiliproteins were extracted from *P. palmata* according to the protocol by Kursar et al. [33] with modifications by Plastino and Guimarães [34]: 300 mg of wet biomass was used per replicate, the

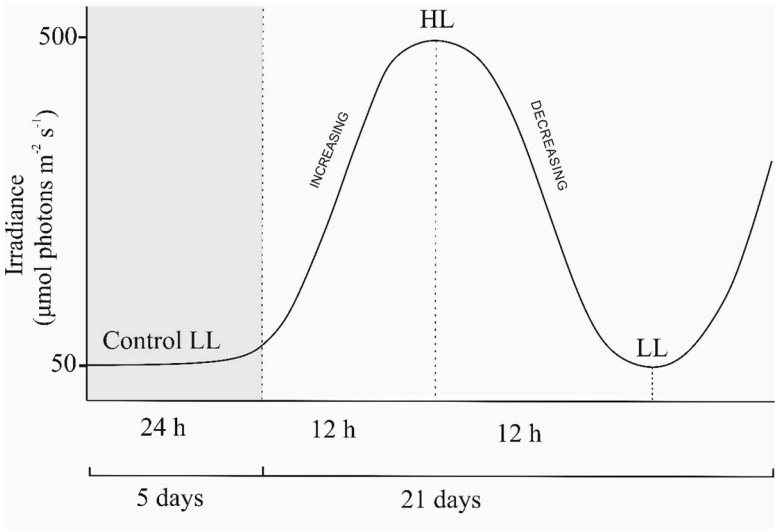

Fig. 1. Experimental low light/high light cycle for exposure of specimens of *Palmaria palmata* at three salinities. (a) The grey band shows the "Pre-control treatment" period (5 days) at 50 µmol photons m^{-2} s^{-1}. Subsequently, the daily light cycle is shown, with the lowest irradiance (LL) at 50 µmol photons m^{-2} s^{-1} and highest irradiance (HL) at 500 µmol photons m^{-2} s^{-1}, increasing and decreasing every 12 h over 21 days.

samples were pulverized with liquid nitrogen and subsequently diluted in 50 mM phosphate buffer, pH 5.5 at 4°C to obtain the supernatant after centrifugation at 11.000 rpm. Absorbence was measured using a UV-Visible Spectrophotometer (Genesys 150, ThermoFisher, USA). The concentration of phycobiliproteins was determined by the equation given by Kursar et al. [33], the absorbances used were 498.5, 614, and 651 nm, to obtain the concentrations of Phycoerythrin (PE), Phycocyanin (PC), and Allophycocyanin (APC), expressed in µg g^{-1} dry weight (DW).

2.5. Antioxidant activity- DPPH

The antioxidant activity was determined using the DPPH assay (2.2-diphenyl-1-picrylhydrazyl). - DPPH is a free radical used in plant extracts to determine radical scavenging activity by hydrogen donation [35, 36]. For this study, the antioxidative potential was determined following the methodology by Springer et al. [37]. Lyophilized material of 50 mg dry weight (DW) ($n = 3$) was extracted in 1 ml of 70% acetone for 24 h under rotary shaking at 4 °C in the dark. The DPPH (2, 2-diphenyl-1-picrylhydrazyl; Sigma-Aldrich, Seelze, Germany) free radical assay was applied, following the protocol of Brand-Williams et al. [38], and modified by Cruces et al. [39]. Trolox (6-hydroxy-2,5, 7,8-tetramethylchroman-2carboxylic acid; Sigma-Aldrich, Seelze, Germany) was used as a standard solution. Triplicate samples were measured in a microplate reader (FLUOstar OPTIMA; BMG Labtech GmbH, Ortenberg, Germany), detecting the absorbence at 520 nm after 15 min. In addition, the antioxidant activity values were expressed as Trolox equivalent TE (mg g^{-1} DW).

2.6. Statistical analysis

To provide an understanding of the effect of salinity on the regulation of the daily photosynthetic cycle, the following analysis were performed on the data set: The normality of variances was tested using the Shapiro-Wilk test, while homogeneity was tested using the Bartlett test. Using these tests, two families of data were exposed: with a normal distribution (F_v/F_m, Chl *a*, Lut, Zeax, APC, PE, PC), and with Gamma distribution (NPQ, β - Car, DPPH, Lut: Chl *a*, Zeax: Chl *a*, β - Car: Chl *a*). Data with normal distribution were used analysis of variance (ANOVA), two-way ANOVA ($p < 0.05$) in the case of phycobilins, while the other data were analysed by a three-way ANOVA ($p < 0.05$). Regarding the data with Gamma distribution, these were analysed by a multifactorial analysis by Generalized Linear Models (GLM) ($p < 0.05$), the full model included three factors: time, salinity, and irradiance. Finally, a Tukey's post hoc test was performed for pairwise comparisons for the whole dataset analysed. All analyses were performed with R 4.10 statistical software.

3. Results and discussion

3.1. Photosynthetic performance

Overall, the diurnal patterns in the regulation of optimum quantum yield (F_v/F_m) did not show significant differences at the end of the experiment, indicating a rapid acclimation process to the light factor (Fig. 2, Supp. Mat. 1). However, over time quantum yield, both for LL and HL, in *P. palmata* showed a decrease with decreasing salinity. Significant differences in quantum yield were observed between S_A 34 and treatments at S_A 28 and 18 (Fig. 2, Supp. Mat. 1). Low photosynthetic optimum quantum yield (F_v/F_m) values due to decreasing salinity have been observed in algae in previous studies on Arctic seaweeds [10, 40] including *Laminaria solindungula* [41]. Diehl et al. [10] show how photosynthetic performance under hyposaline conditions can be maintained during a restricted period of time in brown algae.

Non-photochemical quenching (NPQ) represents a rapid response of the photosynthetic membrane to excess light in PSII [42, 43]. In our study, NPQ increased slightly during the 21 days of culture in the presence of LL and HL. However, under LL, values were lower at all three salinities tested, but significant differences between LL and HL were only observed at S_A 18 on days 1 and 21 (Fig. 3a, Supp. Mat. 2). It is worth noting the high NPQ onset values in *P. palmata* show a high acclimation capacity both in the presence of LL and HL. This result is consistent with that described by Runcie and Riddle [44] for *Iridaea mawsonii*, which reacts quickly to high irradiance by high NPQ values, unlike species such as *Palmaria decipiens* or *Monostroma hariotii* that showed a rather low acclimation capacity. However, in our study, NPQ is mainly affected by salinity variations. Apparently, at lower salinity S_A 28 and 18, a decrease in NPQ at day 21 of culture was observed for both LL and HL, showing significant differences between day 1 and 21 of culture (Fig. 3b, Supp. Mat. 2). The S_A 18 treatment presented the most pronounced differences in NPQ between days 1 and 21 (Fig. 3c, Supp. Mat. 2). In general, the decrease in NPQ in hyposaline conditions agrees with what was observed for the rhodophyte *Stylonema alsidii* by Nitschke et al. [45]. Samples obtained from a marine population exhibited a reduction in

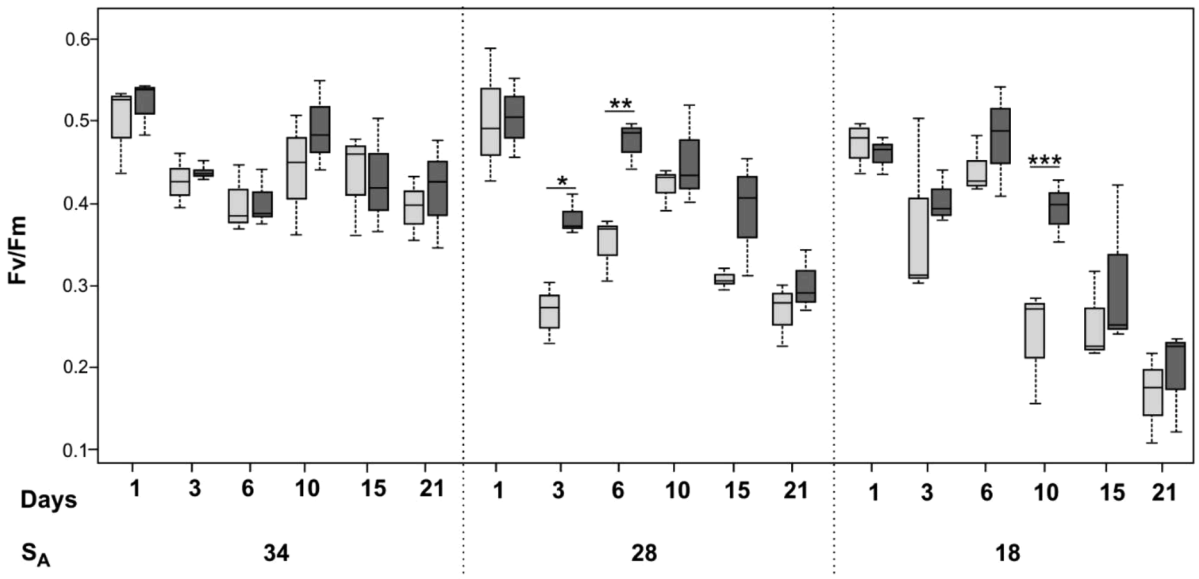

Fig. 2. Mean±SD for F_v/F_m ($n = 3$) in *Palmaria palmata*. Samples at three different salinities (S_A 34, 28, and 18) and two different light points: LL at 50 µmol photons m^{-2} s^{-1} (dark grey) and HL at 500 µmol photons m^{-2} s^{-1} (light grey). Measurements are represented from days 1 to 21. An asterisk indicates statistically significant values between LL and HL: (***) $p<0.0001$, (**) $p<0.001$, (*) $p<0.01$.

NPQ in salinities at S_A 15 and 5, demonstrating its low capacity to acclimation to these factors.

The non-photochemical quenching (NPQ) regulation at S_A 34 was markedly affected by the light factor (LL and HL). At lower salinity, *P. palmata* regulation is strongly affected, with the alga shifting the focus of regulation to salinity variations by day 21. However, *P. palmata* decreased the capacity of regulation at S_A 18. On the other hand, Demmig-Adams et al. [42] suggest that the NPQ mechanism is strongly related to the formation of the pigment zeaxanthin, which is responsible for triggering non-photochemical quenching.

3.2. Photosynthetic pigments

As a primary pigment, Chl *a* was observed in high concentration in *P. palmata* and, on the first day of the experiment, showed a high concentration under LL at S_A 34 and 28 (Fig. 4a, Supp. Mat. 1). Significant differences were only observed for S_A 34 compared to S_A 28 and 18. After 21 days of culture, it can be observed that there is a decrease in concentration for the measured LL and HL samples in all three treatments. In daily light cycles in the species *Chondrus crispus*, it was observed how Chl *a* concentration can be adjusted depending on the high or low irradiance present during the day in a short-term acclimation process [46]. In our study, however, at 21 days at salinities S_A 34 and 28, it is possible to observe a high concentration for HL and the opposite for LL, showing significant differences between both light intensities. For S_A 18, a general decrease in Chl *a* concentration was observed during the 21 days of culture, with no significant differences between LL and HL at the end of the experiment. In general, the pigment Chl *a* is essential in the photosynthetic process, acting as a photocatalyst for energy input to photosystem PSI and PSII [47]. In our study, Chl *a* content in *P. palmata* showed a high acclimation capacity to different LL and HL irradiances at S_A 34 and 28. In contrast, this capacity for acclimation was diminished at S_A 18, in which samples showed significant bleaching due to the loss of pigment.

When comparing Chl *a* concentration between salinities at day 21 of culture, it was observed that under HL at S_A 18 samples presented a lower concentration than under HL at S_A 34 and 28, showing significant differences (Fig. 4a, Supp. Mat. 1). Studies in plants show how variations in salinity can result in the generation of reactive oxygen species (ROS), which directly affect Chl *a* by degrading it and causing a decrease in its concentration in tissues [48–50]. In general, the Chl *a* is a key pigment in the photosynthetic process, and during this study, it can be observed that it is strongly reactive to changes in irradiance and low salinities.

In general, lutein in *P. palmata* exhibited the second-highest concentration after Chl *a* during this experiment. This high concentration coincides with that described by Esteban et al. [51] for this species, where lutein represents 63.7% of the carotenoid composition analysed. Our study observed an increasing trend in lutein concentration in S_A 34 and 18 at 21 days of culture (Fig. 4b, Supp. Mat. 1). Over time, at 21 days of culture, significant differences were only observed between LL and HL in SA 34. Regarding the pigment Lut: Chl *a* ratio and the comparison between LL and HL by salinity, significant differences were only observed in S_A 28 due to increased values in LL (Table 1, Supp. Mat. 2). Lutein is present in high concentrations in algae and plants [52, 53]. In red algae, it is commonly present and, in some groups, could be a functional substitute for zeaxanthin [53–56]. During this study, the decrease in lutein concentration has been shown to be strongly related to an increase in NPQ: García-Plazaola et al. [57, 58] described how the modulation of photoprotective thermal energy dissipation in the NPQ process is correlated with high lutein concentration, thus modulating the photoprotective system.

When comparing salinities, it was observed that LL at S_A 34 presented an increment in the concentration compared with S_A 28 and 18, showing significant differences between S_A 34 with S_A 28 and 18. On the other hand, no significant differences were observed for the HL intensity at different salinities (Fig. 4b, Supp. Mat. 1). When comparing between salinities for Lut: Chl *a* ratio, no significant differences were observed between salinities at day 21.

The regulation of photoacclimation during the daily cycle of *P. palmata* analysed during this experiment is affected by salinity dilution. Therefore, at the end of the cultured period, low salinity marks a decrease in lutein concentration, which directly impacts on the NPQ regulation process as a photoprotective function (Fig. 3c; Suppl. Mat. 2).

Zeaxanthin in *P. palmata* during this study was present in low concentration (Fig. 4c, Supp. Mat. 1). The presence of the zeaxanthin epoxidase (ZEP) gene in the class Florideophyceae has been described by [53]. In general, this carotenoid can be found in red algae but in low concentrations [59]. Esteban et al. [51] did not find its presence in *P. palmata*. On the other hand, work by (Sagert and Schubert [22, 60] and Robertson et al. [61] shows the presence of the pigment zeaxanthin

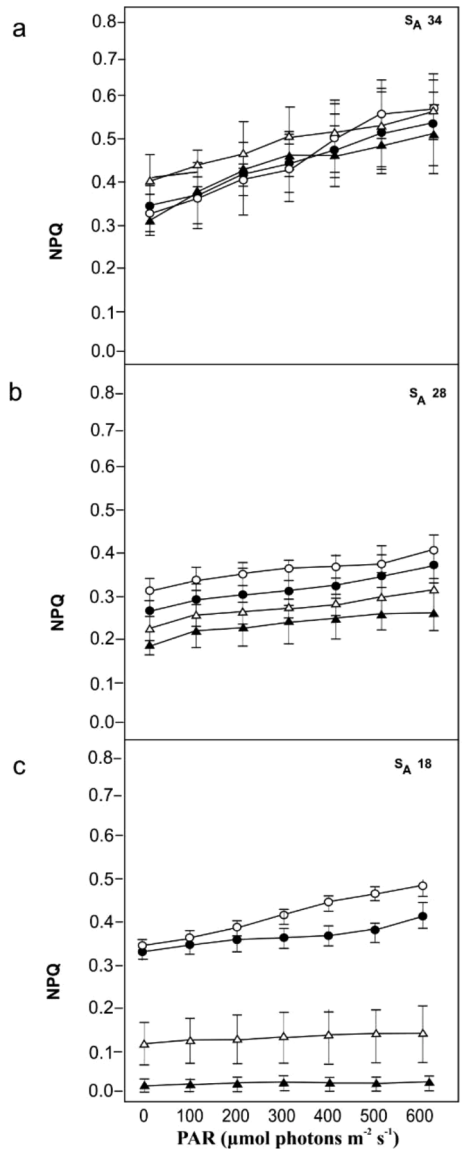

Fig. 3. Mean±SD of NPQ (n = 3) for *Palmaria palmata*. Measurements plotted for days 1 (circles) and 21 (triangle). Two light points are LL at 50 µmol photons m^{-2} s^{-1} (black) and HL at 500 µmol photons m^{-2} s^{-1} (white). Measurements were performed at the three salinities analysed (S_A 34, 28, and 18).

in *P. palmata* albeit in low concentrations. During the culture period, zeaxanthin increased with HL at S_A 28 and 18 after 21 days of culture, showing significant differences with LL during the culture process and at the end of culture (Fig. 4c, Supp. Mat. 1). At S_A 34, this pigment showed no differences between LL and HL during the experiment. On the other hand, increased irradiance did cause a decrease in the Zeax: Chl *a* ratio at S_A 34 and 28 (Table 1; Suppl. Mat. 2). This type of acclimation response has been observed previously in species of the Gracilariales family Rmiki et al. [62] described how dark-adapted species present low percentages of zeaxanthin content *e.g. Gracilaria multipartita* presented 55% and *G. gracilis* 68% zeaxanthin of total xanthophylls, while light-adapted species such as *Gracilariopsis longissima* presented 100% of zeaxanthin.

On the other hand, when comparing by salinity at 21 days of culture, only significant differences in zeaxanthin content were observed between HL at S_A 34 and 28 (Fig. 4c, Supp. Mat. 1). The most pronounced increase in zeaxanthin concentration at HL was observed at S_A 28, generating a separation in concentration levels between LL and HL and resulting in significant differences by day 21 of culture. The decrease in salinity during this study at S_A 28 increased zeaxanthin, presumably as a process of acclimation in *P. palmata*. As observed in this study, short-term acclimation to external factors generates modifications in membrane pigmentation, composition, and functionality [63].

For *P. palmata*, β-carotene levels measured at day 1 showed a higher concentration in HL compared to LL in the three salinities analysed, exhibiting significant differences (Fig. 4d, Supp. Mat. 2). Subsequently, the concentration in HL and LL tends to decrease with time in all salinities; however, there is a tendency for β-Carotene to be higher at HL, showing significant differences on some days measured during the 21 days of culture. However, on day 21, differences were only observed between LL and HL at S_A 34, with the highest concentration observed at the latter irradiance. On the other hand, the ratio β – Car: Chl *a*, at the beginning of the experiment, showed high values for HL and low values for LL at all salinities (Table 1, Supp. Mat. 2). Subsequently, the opposite pattern was observed over time, with a decrease in HL values and an increase in LL. Significant differences were only observed on day 21 between LL and HL in S_A 34 and 28. It should be noted that carotenoids such as β-Carotene have an antioxidant function, mainly in periods of high irradiance, hence serving as a photoprotector [64, 65]. The increase of this carotenoid during exposure to S_A 28 and 18 might indicate that susceptibility to high irradiance levels increase with reduced salinity. However, at the end of these treatments, samples showed no differences, which shows the loss of regulation at high irradiance due to the decrease in salinity.

Phycobiliproteins are strongly linked to changes in irradiance [66]. Variations with irradiance changes were observed in *P. palmata* during this experiment, at day 21 of culture in the three salinities analysed as there was a higher concentration at HL (Table 1, Supp. Mat. 3). The phycoerythrin (PE) pigment increased in concentration at day 21 at HL, with significant differences between LL and HL at S_A 28 and 18. Subsequently, when LL was analysed at the three salinities, a decrease in concentration was observed at S_A 28 and 18 compared to S_A 34 (Table 1, Supp. Mat. 3). Sagert et al. [46] described how the red alga *Chondrus crispus* can effectively regulate phycobilin concentration during daily cycles. A decrease in phycoerythrin concentration can be observed after exposure to light periods in samples from 3 to 5 m depth. A daily regulation around the light cycle is in agreement with what was observed for *P. palmata* during this study; however, a high concentration was observed during exposure to HL and not afterward, as in the case of *C. crispus*.

Concerning allophycocyanin concentration (APC) at day 21 of culture, significant differences could be observed between LL and HL, at S_A 28 and 18. Significant differences were only observed in LL values when comparing salinities, with a decrease in values at lower salinity (Table 1, Supp. Mat. 3). However, the reduction in allophycocyanin concentration around low salinity does not agree with the observations of Burdett et al. [67], who described for the red alga *Lithothamnion glaciale* that phycobiliprotein composition and concentration does not vary with decreasing salinity.

Finally, phycocyanin (PC) at day 21 showed low concentrations at all three salinities analysed. Significant differences between LL and HL at S_A 18 in *P. palmata* were recorded. As for APC, low concentrations were observed for LL at S_A 28 and 18 during this experiment (Table 1, Supp. Mat. 3). Contrary to observations made in short-term studies such as this one, long-term studies in *P. palmata* have shown that high irradiance negatively affects phycobiliprotein concentration [16]. In the case of *P. palmata*, changes in phycobiliprotein concentration show the activation of the dynamic acclimation process to irradiance variations present in the short-term daily cycles. At the same time, the decrease in phycoerythrin and allophycocyanin values at lower salinity shows that the acclimation process of *P. palmata* is not very robust in terms of pigmentation and cannot effectively withstand decreases in salinity.

Table 1 Pigment ratio and concentration measured (n = 3) for *Palmaria palmata* at day 21. Samples at three different salinities (S_A 34, 28, and 18) and two different light points LL at 50 µmol photons m^{-2} s^{-1} and

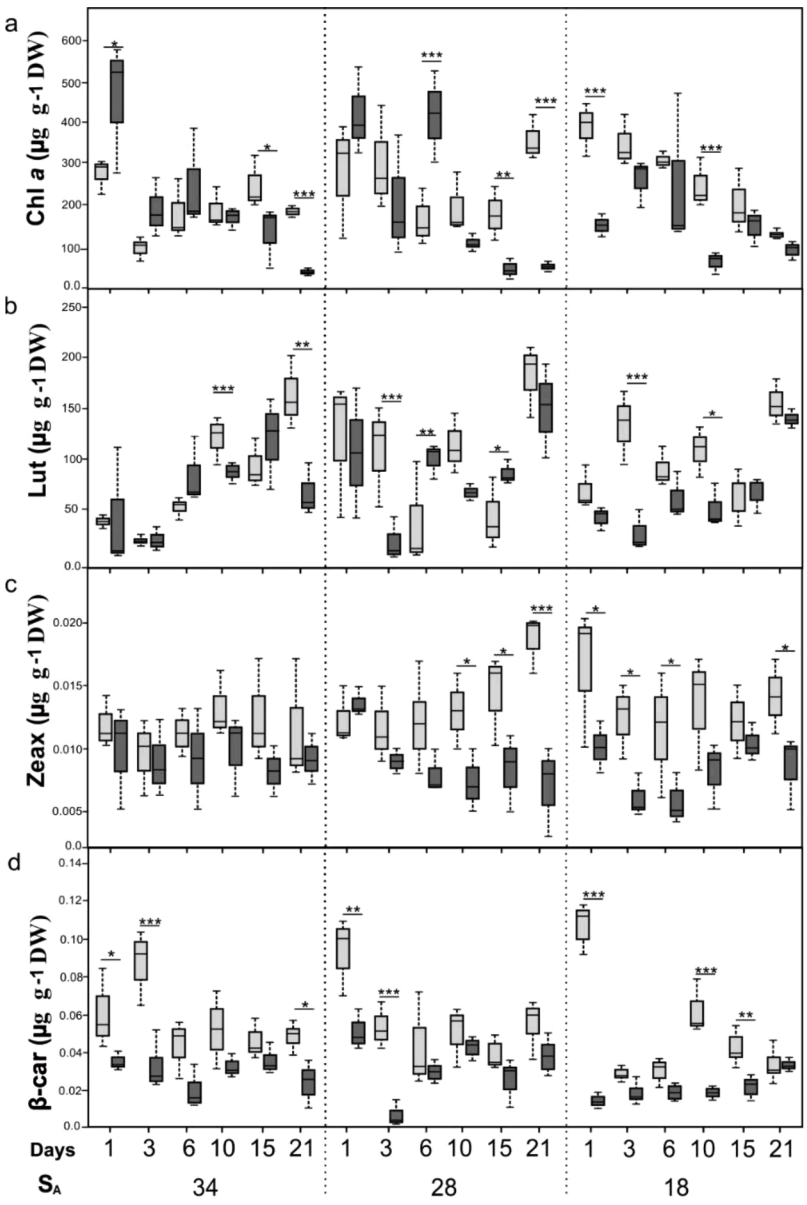

Fig. 4. Mean±SD pigment concentration (n = 3) in *Palmaria palmata*. For pigments, Chlorophyll *a* (Chl *a*), Lutein (Lut), Zeaxanthin (Zeax), and β-Carotene (β-Car) in (µg g^{-1} DW). Samples at three different salinities (S_A 34, 28, and 18) and two different light points LL at 50 µmol photons m^{-2} s^{-1} (dark grey) and HL at 500 µmol photons m^{-2} s^{-1} (light grey). Measurements represented from days 1 to 21. An asterisk indicates statistically significant values between LL and HL: (***) $p<0.0001$, (**) $p<0.001$, (*) $p<0.01$.

Table 1
Pigment ratio and concentration measured ($n = 3$) for *Palmaria palmata* at day 21. Samples at three different salinities (S_A 34, 28, and 18) and two different light points LL at 50 µmol photons m^{-2} s^{-1} and HL at 500 µmol photons m^{-2} s^{-1}. Pigment ratios Lut: Chl *a*, Zeax: Chl *a* and β-Car: Chl *a*, and pigment concentration Allophycocyanin (APC), Phycoerythrin (PE) and Phycocyanin (PC); all values given as µg g^{-1} (DW). Different letters indicate significant differences between light points ($p < 0.05$).

S_A	Light Points	Lut:Chl *a*	Zeax:Chl *a*	β-Car:Chl *a*	APC (µg g^{-1} DW)	PE (µg g^{-1} DW)	PC (µg g^{-1} DW)
34	LL	1.59(±0.54)^a	0.11(±0.01)^a	0.59(±0.26)^a	22.70(±8.05)^a	64.94(±10.71)^a	6.16(±3.29)^a
	HL	0.82(±0.15)^a	0.05(±0.03)^b	0.25(±0.03)^b	26.21(±10.67)^a	69.75(±17.44)^a	7.99(±3.44)^a
28	LL	2.95(±0.38)^a	0.10(±0.06)^a	0.76(±0.04)^a	8.19(±1.71)^b	24.62(±3.34)^b	1.99(±1.17)^b
	HL	0.50(±0.06)^b	0.05(±0.03)^b	0.15(±0.04)^b	26.34(±11.73)^a	59.55(±22.60)^a	7.87(±4.51)^a
18	LL	1.64(±0.44)^a	0.21(±0.08)^a	0.39(±0.15)^a	4.75(±0.76)^b	22.72(±3.13)^b	0.92(±0.74)^b
	HL	1.19(±0.06)^a	0.14(±0.07)^a	0.27(±0.07)^a	18.70(±4.46)^a	39.88(±9.86)^a	6.17(±0.22)^a

HL at 500 µmol photons m^{-2} s^{-1}. Pigment ratios Lut: Chl *a*, Zeax: Chl *a* and β-Car: Chl *a*, and pigment concentration Allophycocyanin (APC), Phycoerythrin (PE) and Phycocyanin (PC); all values given as µg g^{-1} (DW). Different letters indicate significant differences between light points ($p < 0.05$).

3.3. Antioxidant activity

Antioxidant activity in *P. palmata* increased at HL to S_A 34 at day 21 of culture. It was also possible to observe a general increase in HL values at day 21 of culture in the three salinities tested, with significant differences observed (Fig. 5, Supp. Mat. 2).

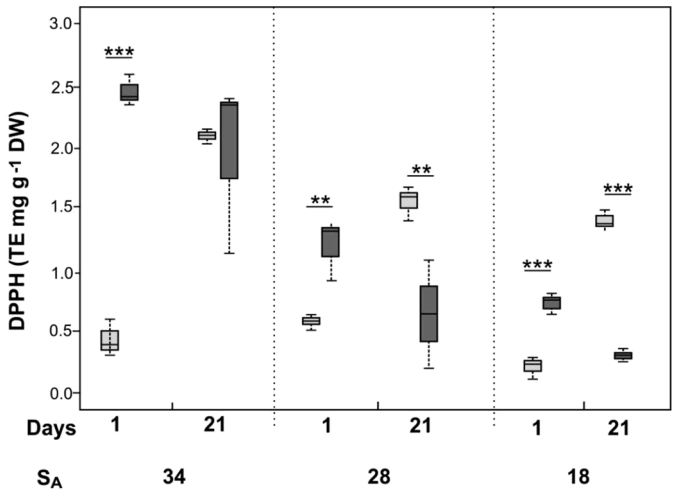

Fig. 5. Antioxidant activity DPPH Mean±SD (n = 3) in *Palmaria palmata*. Samples at three different salinities (S_A 34, 28, and 18) and two different light intensities LL at 50 µmol photons m^{-2} s^{-1} (dark grey) and HL at 500 µmol photons m^{-2} s^{-1} (light grey). Measurements represented for days 1 and 21. An asterisk indicates statistically significant values between LL and HL: (***) $p<0.0001$, (**) $p<0.001$, (*) $p<0.01$.

High antioxidant activity was previously recorded for *P. palmata* in Kongsfjorden, Arctic, by Dummermuth [68]. This study mentions the close association of the antioxidant response with the habitat where it is found, which is mainly the upper sublittoral, being able to regulate its activity on a daily basis. On the other hand, when comparisons were made between salinities, the measurements during LL and HL decreased with lower salinity (Fig. 5, Supp. Mat. 2).

The results obtained in this study also have implications at the ecosystem level. In general, zeaxanthin and lutein are affected by decreased salinity in *P. palmata* and may interfere with the process of thermal energy regulation by NPQ. *Palmaria palmata*, mainly distributed in cold/temperate waters of the North Atlantic [25], towards the coasts of Europe, inhabits the Atlantic coast, up to the entrance of the Baltic Sea (Kattegat coasts), its range being limited by to the decreasing salinity in this area [20, 69, 70]. Therefore, salinity strongly controls the distribution of *P. palmata*. Populations that have been described for the Baltic Sea are specifically adapted to hyposalinity, being able to maintain a high growth rate in S_A 20 and 15, provided that the nutrient concentration is high [20, 70]. However, it remains to be seen what effect a progressing hyposalinity regime in Arctic fjords will have on populations that are not adapted. Karsten et al. [25] described how *P. palmata* at S_A 15 bleaches, showing a poor acclimation capacity to external salinity. Baral [12] describes how *Saccharina latissima* populations in the presence of hyposaline conditions will be limited in their distribution and growth in the Arctic zone in the future, even though the increase in temperature is beneficial for the development of the alga as such.

4. Conclusion

The physiological response of the rhodophyte *Palmaria palmata* to daily fluctuations in irradiance shows an overall broad tolerance range, which becomes progressively restricted with decreasing salinity, as typically being the case in Arctic fjords under summer conditions. Acclimation to hyposaline conditions generates a high energy demand. In the future, this energy demand might be reflected by a reduction in the growth rate of *P. palmata* and a decline in its populations in the Arctic or, eventually counteracted *i.e.* by the development of a low-salinity resistant ecotype such as those found at the Baltic Sea entrance [20].

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jpap.2022.100124.

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