Differential acclimation responses to irradiance and temperature in two co-occurring seaweed species in Arctic fjords

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Abstract

Arctic fjord systems experience large amplitudes of change in temperature and radiation regime due to climate warming and the related decrease in sea ice. The resultant increase in irradiance entering the water column influences photosynthetic activity of benthic and pelagic primary producers. The subtidal brown alga *Desmarestia aculeata* and the intertidal red alga *Palmaria palmata* populate the cold-temperate coasts of the North Atlantic, reaching the polar zone. To evaluate their acclimation potential, we collected both species in Kongsfjorden, Svalbard (78.9°N, 11.9°E), during the Arctic summer and exposed specimens to two different PAR levels (50 and 500 µmol photons m^{-2} s^{-1}) and temperatures (0, 4 and 8 °C) for 21 days. Photosynthetic parameters and biochemical features (pigment concentration and antioxidants) were assessed. In general, high irradiance was the factor that generated a negative effect for *D. aculeata* and *P. palmata* in the photosynthetic parameters of the photosynthesis–irradiance curve and F_v/F_m. The pigment concentration in both species tended to decrease with increasing irradiance. Antioxidant level showed different trends for both species: in *D. aculeata*, antioxidant potential increased with high irradiance and temperature, while in *P. palmata*, it only increased with high irradiance. Both species showed responses to the interaction of irradiance and temperature, although *D. aculeata* was more sensitive to high irradiance than *P. palmata*. Our study shows how these species, which have similar geographical distribution in the North Atlantic and the Arctic but belong to different taxonomic lineages, have similar strategies of acclimation, although they respond differently to ecophysiological parameters.

To access the supplementary material, please visit the article landing page

Introduction

The Arctic is characterized by a dynamic climate history, which has been marked by several glacial processes (Miller et al. 2009). The current warming process in the Arctic is two times higher than the global average, and this condition is strongly related to the increase in surface air temperature (He et al. 2019), also called Arctic Amplification (Serreze & Francis 2006; He et al. 2019). The Svalbard archipelago is currently considered as a model

region for studies of transitions in the atmospheric, terrestrial and marine realm. Here, the fjord Kongsfjorden has been particularly intensively studied as a natural laboratory to observe climate imprints on marine Arctic communities (Wiencke & Hop 2016), and it has been suggested as a harbinger of change in a pan-Arctic perspective (Bischof et al. 2019).

In the coastal habitat of Arctic fjord systems, macroalgae represent ecosystem engineering organisms of utmost ecological significance, and the response of macroalgal communities towards environmental change is crucial for future ecosystem function particularly in high-latitude fjord systems (Krause-Jensen et al. 2015). In these habitats, macroalgal communities are under strong control by seasonally changing abiotic drivers. Francis & Hunter (2006) describe how the increase in temperature over the past few decades has led to a significant decline in Arctic sea-ice cover, and Wiencke et al. (2006) described how sea-ice conditions modulate the underwater radiation climate. This has raised a number of questions, mainly related to the effect of light availability on photosynthesizing organisms in the water column and on the seafloor (Hanelt et al. 2001). Macroalgae in the Arctic have to react to strong seasonal variations and have, therefore, developed a wide range of physiological plasticity (Karsten et al. 2003). Bringloe et al. (2020) highlight the complex evolutionary process of marine benthic species around the Arctic, suggesting that a large number of algal species do not simply tolerate high latitude conditions but are adapted to them.

The Kongsfjorden area is increasingly influenced by the warm water current coming from the western Atlantic, generating a strong interface with the characteristics of High-Arctic waters (Bischof et al. 2019). Kongsfjorden's algal community is likely to change in correspondence to the specific temperature requirements of the species involved (Bartsch et al. 2016). In contrast to the Antarctic marine flora, Arctic-dwelling macroalgal species exhibit a low level of endemism (Wulff et al. 2011), and most of the inhabiting species are cold-tolerant extensions of populations found in temperate zones (Bringloe et al. 2020). However, to thrive in such high latitudes, macroalgal species have to be adapted to cope with strong seasonality in light climate and year-round low temperatures (Wiencke et al. 2011; Zacher et al. 2011; Wiencke & Amsler 2012). Overall, Arctic fjord systems are marked by high macroalgal species diversity, and Fredriksen et al. (2019) reported a total of 197 macroalgal species for the Svalbard archipelago, with 84 species occurring in Kongsfjorden. Ongoing changes in abiotic drivers will presumably affect competitive interactions among macroalgae and generate shifts in community structure.

Besides kelp, the phaeophyte *Desmarestia aculeata* (Linnaeus) J. V. Lamouroux and the rhodophyte *Palmaria palmata* (Linnaeus) Kuntze (Rhodophyta, Palmariaceae) are frequently present in Arctic fjord systems but rarely studied at this high latitude. *Palmaria palmata* has a distribution around the North Atlantic Ocean, mainly found in rocky shore environments, from the intertidal to the shallow subtidal zone (MacArtain et al. 2007; Bjarnadóttir et al. 2018). A large number of studies of *P. palmata* in North America and Europe are strongly related to its use in the feeding of abalone in hatcheries (Le Gall et al. 2004). It is also sought after for its high content of fibre, vitamins, minerals, proteins (Lahaye et al. 1993) and antioxidants (Wang et al. 2010) and for its anti-inflammatory effects (Lee et al. 2017).

Desmarestia aculeata mainly inhabits the subtidal zone, is an opportunistic alga at the time of habitat colonization and is frequently found in association with other species in the same genus (Kain & Jones 1975) as well as other large brown algae, such as *Saccharina latissima*, *Laminaria hyperborea*, among others (Pehlke & Bartsch 2008). This species has previously been included in ecological studies and species lists in the North Atlantic, for example, by Mathieson & Dawes (2017) and Nielsen & Lundsteen (2019), who conducted a review of the genus *Desmarestia* off the coast of Russia. Some specific studies have been carried out on the species *D. aculeata*, both in the laboratory and in the field, in order to understand ecophysiological patterns in relation to the seasonality of the species (Chapman & Burrows 1970; Bischof et al. 2002).

Both *D. aculeata* and *P. palmata* have a perennial life cycle (Hop et al. 2002) and, therefore, undergo a series of adaptive adjustments to cope with the changes in irradiance and temperature during the course of the year. In general, the photosynthetic rate of Arctic macroalgae is affected by a series of abiotic factors (Hurd et al. 2014). Although irradiance is a vital factor for these organisms, excess light can generate photoinhibition (Hurd et al. 2014). This is mainly due to the photo-oxidation of photosynthetic pigments and proteins, by the formation of ROS, increased fragmentation of photosystem II or decreased turn-over of the D1 protein (Aro et al. 1993). With regard to temperature, macroalgae in the Arctic are generally not strictly adapted to low temperatures (Hurd et al. 2014), with the exception of some Arctic endemic species, such as *Laminaria solidungula* (Dunton & Dayton 1995). Variations in temperature directly influence developmental processes, for example, spore germination (Müller et al. 2008). The wide distribution range of most species found in the Arctic suggests that increased temperature will not be a determining factor in the survival of these species per se (Hurd et al. 2014). However, it is expected that increases in temperature may affect other

environmental variables, which may, in turn, affect the ecology of the species in a negative or positive way.

The large number of studies carried out on species that form underwater forests (kelps) in the High Arctic contrasts with the scarcity of ecological and physiological studies of other macroalgal species that are associated with these forests or their peripheries and that might also play an important role in ecological networks. So far, the focus of research on *P. palmata* in the Arctic has been mainly on physiology (Hanelt & Nultsch 1995; Holzinger et al. 2004), UV effects (Karsten & Wiencke 1999; Van De Poll et al. 2002; Karsten et al. 2003) and the seasonal variation of ecophysiological patterns (Aguilera et al. 2002). Arctic specimens have also been studied with respect to their responses to increased temperature and CO_2 (Gordillo et al. 2016). Still, many aspects involved in the acclimation process of *P. palmata* in a changing Arctic are unresolved.

The brown alga *D. aculeata* is another species found in the Arctic that has been less studied, although it is abundant and ecologically valuable (Lippert et al. 2001). Some studies conducted on this species in the Arctic have focused on seasonal variation and biochemical response to increased light intensity (Aguilera et al. 2002) and on its response to increased CO_2 combined with increasing temperature (Iñiguez et al. 2015; Gordillo et al. 2016).

The main objective of the present study was to investigate the effects of the combined change in two environmental drivers—temperature and irradiance—on *D. aculeata* and *P. palmata*, two understudied macroalgal species in a High-Arctic fjord system. For both species, we studied the consequences of variation in temperature and irradiance to photosynthetic performance and set out to reveal the physiological adjustments and limits of acclimation. On the basis of their similar geographic distribution, but with slightly different vertical habitat preference, we hypothesized that both species will most likely not be adversely affected by the current increase in temperature in the Arctic but might respond differently with respect to variation in light.

Material and methods

Two species of Arctic seaweeds were collected for this study, *Desmarestia aculeata* and *Palmaria palmata*. The experiment was carried out in July 2019 in the Kings Bay Marine Laboratory, Ny-Ålesund, Spitsbergen, Svalbard (78.9 N, 11.9 E; Supplementary Fig. S1). Algal material was collected at two sites. Specimens of *D. aculeata* were collected at Brandal (78°56′49.25″N; 11°51′25.03″E) by SCUBA diving at 5–6 m depth, and specimens of *P. palmata* were collected in the shallow subtidal in front of the Marine Laboratory (78°55′39.8″N; 11°55′48.3″E) at 0–1 m depth (Supplementary Fig. S1). For both species,

apical fragments from vegetative fronds were selected. For *D. aculeata*, young sporophytes were used, while for *P. palmata*, vegetative gametophyte material was collected.

Fronds of both species were maintained in a "pre-control treatment," in 1-L seawater (34 psu) tanks enriched with PES-Provasoli; the medium was renewed every four days. Control samples were under constant illumination at 50 µmol photons m^{-2} s^{-1} and at three different temperatures 0, 4 and 8 °C for seven days. After this period of acclimation, some of the fronds were maintained in control light conditions, and the other fronds were transferred at 500 µmol photons m^{-2} s^{-1} for a period of 21 days. Three independent replicate fronds were used per treatment.

Photosynthetic performance

Variable chl *a* fluorescence of PSII was measured with a pulse amplitude-modulated chlorophyll fluorometer (Imaging PAM, Walz). The maximal quantum yield of PSII (F_v/F_m) was measured after 10 min of dark-adaptation. Immediately after, rapid light curves (P-E) were measured: algal samples were irradiated with an increasing actinic irradiance (between 0 and 600 µmol photons m^{-2} s^{-1}) every 30 s (Schreiber et al. 1995). From the P-E curves, the following parameters were calculated: photosynthetic capacity expressed as maximum relative electron transport rate (rETRmax), saturation irradiance (*E*k) and photosynthetic efficiency (α, initial linear slope). The hyperbolic (P-E) curves were fitted according to the equation of Platt et al. (1980), using the KaleidaGraph version 4.0 (Synergy Software).

Pigment analyses

The extraction of photosynthetic and accessory pigments (*n* = 3) was performed following the method of Koch et al. (2015). Algal material was frozen in liquid nitrogen, lyophilized for 24 hr and pulverized for 20 s in a high-speed homogenizer (Fast prep®-24; MP Biomedicals). Between 0.05 and 0.1 g of biomass was extracted in 1 ml acetone (90%, v/v), and the samples were kept at 4 °C for 24 hr in darkness and finally analysed using a Hitachi LaChromeElite® high-performance liquid chromatography system. The system was equipped with a chilled autosampler L-2200 and a DAD detector L-2450 (VWR-Hitachi International). Separation of pigments was performed according to methods described by Wright et al. (1991) and Diehl et al. (2020).

For *D. aculeata*, the following pigments were measured: chl *a* and chl *c2*, β-car and Fuco, and VAZ, the pigments of the xanthophyll cycle. The DPS of the xanthophyll cycle was calculated according to the method of Colombo-Pallotta et al. (2006).

For *P. palmata*, the following pigments were quantified by HPLC: chl *a*, Lut and β-car. Phycobilipigments were extracted, 300 mg of algal biomass per replicate, and were ground and diluted in 50 mM phosphate buffer, pH 5.5, at 4 °C. This solution was centrifuged for 20 min at 10.000 × g and 4 °C to obtain a phycobiliprotein supernatant. The absorption was measured in a microplate reader (Fluostar Optima, BMG Labtech). The concentration of the phycobilipigments Pe, Apc and Pc was determined by absorption measurements at wavelengths of 498.5, 614 and 651 nm following the equation of Kursar et al. (1983). Pigment concentration was expressed in μg g^{-1} DW.

Antioxidant analysis

The antioxidant activity was measured by applying the free radical DPPH (Sigma-Aldrich) assay, following the protocol of Brand-Williams et al. (1995), and modified by Cruces et al. (2012) and Koch et al. (2016). For the standard solution, the Trolox (Sigma-Aldrich) was used. This analysis was applied for both species, *D. aculeata* and *P. palmata*, and 0.5 mg of freeze–dried biomass per sample (*n* = 3) was used in the extraction. The antioxidant activity of the samples was estimated from triplicate subsamples and expressed as TE (mg g^{-1} DW).

The concentration of phlorotannins in *D. aculeata* was determined as presented by Springer et al. (2017), using the Folin-Ciocalteu method described by Cruces et al. (2012). Purified phloroglucinol (Sigma-Aldrich) was used for the standard. Twenty milligram of freeze–dried biomass per sample (*n* = 3) was extracted in 1 ml of acetone (70% v/v) and kept at 4 °C for 24 hr in darkness. For quantification, absorption was measured at λ = 730 nm in a microplate photometer using three aliquots per replicate. The results were expressed in mg g^{-1} DW.

Results for both species were analysed separately. To test for differences and interactions between temperatures and light treatments, the data were tested for normal distribution (Shapiro-Wilk test; *p* < 0.05). In cases of non-normal distribution, data were log-transformed. For data with normal distribution two-factorial ANOVA, two-way ANOVA was carried out. When the test revealed significant differences, a post-hoc Tukey's HSD test was applied. The statistical analyses were run using RStudio (version 1.1.383, Boston, MA).

Results

Photosynthetic performance

The maximal quantum yield (F_v/F_m) in *D. aculeata* decreased in both irradiances compared to the initial control treatment after 21 days of culture; this was observed at all temperatures. Significant differences were observed between the initial control treatment compared to the 50 and 500 μmol photons m^{-2} s^{-1} treatments at all temperatures. No differences were observed between treatments due to temperature. For *P. palmata*, a significant decrease in F_v/F_m was observed between the initial control and the high light treatment after 21 days at 4 and 8 °C. Also, initial control samples and specimens under 50 μmol photons m^{-2} s^{-1} showed significantly higher values at 8 °C compared to samples at 0 and 4 °C (Table 1, Supplementary Table S1).

Photosynthetic parameters as obtained from P-E curves were affected by the experimental treatments as follows. When comparing α in *D. aculeata*, significant differences were observed between light intensities at 0 °C, as a decrease in values was observed at 50 and 500 μmol photons m^{-2} s^{-1} treatments after 21 days of culture. For α in *P. palmata*, there was a significant decrease in specimens under 500 μmol photons m^{-2} s^{-1} at 0 °C, while at 4 °C, the values tended to decrease at 50 and 500 μmol photons m^{-2} s^{-1} compared to initials. At 8 °C, there were no significant variations observed with respect to light intensity. With regard to temperature, significant differences were observed with the 500 μmol photons m^{-2} s^{-1} treatments at 0 °C and the initial control at 4 °C, compared to the other treatments analysed (Table 1, Supplementary Table S1).

The rETRmax in *D. aculeata* showed a tendency to decrease with increasing light intensity at all temperatures; significant differences were observed between the initial control and the 50 and 500 μmol photons m^{-2} s^{-1} treatments at all temperatures. No significant differences were observed between temperatures.

The increase in light intensity tended to negatively affect the rETRmax values in *P. palmata* at 0 °C, while at 4 °C, the values tended to decrease with both irradiances after 21 days of cultivation; significant differences were observed between the initial control treatment and the other irradiances. With respect to the temperature factor, only significant differences were recorded for the 500 μmol photons m^{-2} s^{-1} treatment at 0 °C and the initial control treatment at 4 °C (Table 1, Supplementary Table S1; two-way ANOVA, Tukey HSD, *p* < 0.05).

In *D. aculeata*, *E*k tended to be lower at 50 and 500 μmol photons m^{-2} s^{-1} when compared to the initial control treatment. This pattern was visible at 0 and 4 °C. At 8 °C, after 21 days of culture, the samples at 50 and 500 μmol photons m^{-2} s^{-1} showed no major variations in *E*k between them and the initial control treatment (Table 1, Supplementary Table S1). *Palmaria palmata* tended to present lower values of *E*k with increasing light intensity at 0 and 4 °C. However, no significant differences between light treatments were observed. Overall, significantly higher values of *E*k were recorded at 0 °C

Table 1. Photosynthetic parameters measured (n=3) for *Desmarestia aculeata* and *Palmaria palmata*: F_v/F_m and the parameters obtained from P-E curves, α, rETRmax and Ek. Measured at three different temperatures (0, 4 and 8°C) and different light intensities: control (initial control measure 50 µmol photons m^{-2} s^{-1}), 50 and 500 µmol photons m^{-2} s^{-1} (after 21 days of culture). Different letters indicate significant differences among treatments ($p < 0.05$).

Temp. (°C)	Treatment	F_v/F_m	Initial slope (α) (µmol photons m^{-2} s^{-1})$^{-1}$	rETRmax (rel. units)	Saturating point (*Ek*) (µmol photons m^{-2} s^{-1})
D. aculeata					
0	Control	0.61 (±0.03)[abc]	0.20 (±0.02)[a]	14.37 (±1.67)[a]	72.58 (±14.33)[ab]
	50	0.41 (±0.02)[de]	0.12 (±0.02)[bc]	10.84 (±2.47)[bc]	64.31 (±13.69)[abcd]
	500	0.14 (±0.02)[e]	0.08 (±0.02)[c]	3.14 (±0.54)[c]	39.81 (±11.29)[cd]
4	Control	0.59 (±0.01)[a]	0.19 (±0.03)[ab]	12.73 (±2.41)[a]	67.74 (±18.80)[abc]
	50	0.53 (±0.05)[bc]	0.24 (±0.02)[abc]	8.47 (±0.77)[bc]	39.24 (±10.69)[bcd]
	500	0.16 (±0.04)[e]	0.12 (±0.04)[bc]	3.06 (±1.04)[c]	26.83 (±5.49)[d]
8	Control	0.60 (±0.01)[ab]	0.17 (±0.03)[ab]	11.58 (±3.63)[a]	68.68 (±16.12)[a]
	50	0.47 (±0.05)[cd]	0.20 (±0.05)[ab]	12.71 (±1.35)[bc]	64.02 (±13.82)[abc]
	500	0.16 (±0.04)[e]	0.13 (±0.05)[bc]	8.68 (±0.76)[b]	69.26 (±18.10)[abc]
P. palmata					
0	Control	0.27 (±0.02)[bc]	0.09 (±0.04)[ab]	4.82 (±0.96)[bcd]	75.91 (±8.91)[ab]
	50	0.27 (±0.01)[bc]	0.08 (±0.02)[ab]	4.75 (±0.37)[bcd]	61.85 (±12.44)[ab]
	500	0.19 (±0.05)[c]	0.05 (±0.02)[c]	2.40 (±0.24)[d]	51.31 (±11.79)[a]
4	Control	0.38 (±0.01)[b]	0.18 (±0.02)[d]	5.92 (±0.69)[ab]	36.55 (±3.80)[bc]
	50	0.31 (±0.02)[bc]	0.15 (±0.01)[abc]	6.16 (±0.66)[bc]	40.08 (±10.01)[c]
	500	0.19 (±0.02)[c]	0.08 (±0.02)[ab]	2.60 (±0.99)[d]	34.94 (±9.48)[c]
8	Control	0.49 (±0.03)[a]	0.09 (±0.04)[ab]	8.03 (±1.07)[a]	57.67 (±12.09)[abc]
	50	0.45 (±0.02)[a]	0.14 (±0.02)[abc]	7.03 (±1.20)[ab]	47.76 (±7.01)[abc]
	500	0.28 (±0.04)[bc]	0.14 (±0.03)[abc]	5.05 (±0.93)[ab]	51.43 (±7.03)[abc]

compared to the 4 °C treatment but not when compared to 8 °C (Table 1, Supplementary Table S1).

Photosynthetic pigments

The variation in pigment composition showed differences with respect to the light and temperature treatments. See Supplementary Table S2 for the results of the statistical analysis (two-way ANOVA, Tukey HSD, $p < 0.05$).

Desmarestia aculeata. The values of chl *a* tended to decrease at higher light intensity at all temperatures (Fig. 1a, Supplementary Table S2). Significantly lower values were recorded under the 500 µmol photons m^{-2} s^{-1} treatment at all temperatures. Variations due to temperature were not recorded in this species (Fig 1a, Supplementary Table S2).

The pigments chl *c2* and Fuco tend to decrease with high light at all temperatures. Chl *c2* values decreased markedly with more light. Significant differences were observed between light treatments for each temperature. No differences were observed between temperatures.

For Fuco, the results showed a tendency to decrease in concentration at higher light and temperature. Significant differences could be observed between light treatments at all temperatures and between the treatment 500 µmol photons m^{-2} s^{-1} at 8 °C, with those at 0 °C and 4 °C (Fig. 1b–c, Supplementary Table S2).

Other pigments in *D. aculeata* such as β-car, Viol and Anthera showed low concentration values and tended to further decrease with high light. For β-car, significant differences were observed between the initial control and the 500 µmol photons m^{-2} s^{-1} treatment at all temperatures (Fig. 1d, Supplementary Table S2). With respect to Viol, the concentration tended to decrease in both light intensities after 21 days of cultivation. Significant differences were observed between treatments of different temperatures. Differences were also observed between the initial control and the 500 µmol photons m^{-2} s^{-1} treatment at 4 and 8 °C (Supplementary Tables S2, S3). For Anthera, differences were only observed at 0 °C between the initial control treatment with the 50 and 500 µmol photons m^{-2} s^{-1} treatments, after 21 days of culture. Finally, significant differences
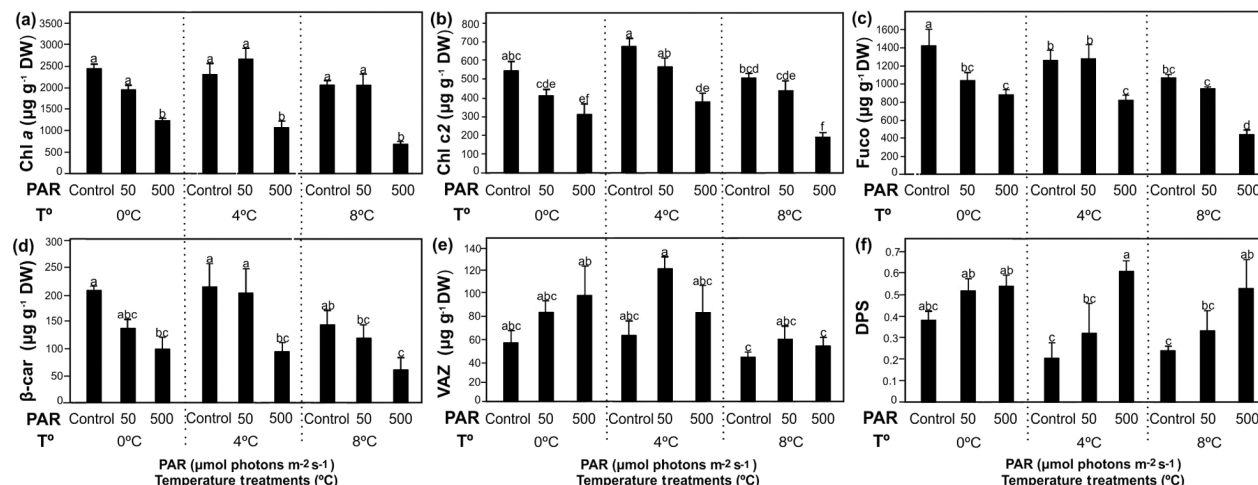
Fig. 1 Mean±SD pigment concentrations (*n*=3) in *Desmarestia aculeata*. For the pigments chl *a*, chl *c2*, Fuco, β-car, the table shows the pool size of the xanthophylls (VAZ) and de-epoxidation status of the xanthophyll cycle (DPS) in (µg g $^{-1}$ DW). Samples at three different temperatures (0, 4 and 8°C) and different light intensities: control (initial control measure 50 µmol photons m^{-2} s^{-1}), 50 and 500 µmol photons m^{-2} s^{-1} (after 21 days of culture). Different letters indicate significant differences among light treatments for temperatures ($p < 0.05$).

were observed between the initial control treatment at 0 °C compared with treatments at 4 and 8 °C (Supplementary Tables S2, S3).

Zeax was present in low concentration, but a tendency for increasing values under high light was identified at all temperatures. Significant differences were observed between the initial control and the 500 µmol photons m^{-2} s^{-1} treatment at all temperatures. The temperature factor caused no significant differences in Zeax content (Supplementary Tables S2, S3).

The overall pool size of xanthophyll cycle pigments (VAZ) was low in all treatments, and no major variations were observed between different light intensities, although significant differences were observed between treatments at 8 °C with 0 and 4 °C (Fig. 1e, Supplementary Table S2).

Pigment ratios of *D. aculeata* were calculated from HPLC data (Supplementary Tables S2, S4). The Fuco:chl *a* pigment ratio tends to show an increase with more light at 4 and 8 °C, but no significant differences were observed. At 0 °C, the initial control showed a significantly higher value compared to the other light treatments. No significant differences were observed between temperatures. The Zeax:chl *a* ratio presented a trend to increase under 500 µmol photons m^{-2} s^{-1} after 21 days of cultivation at all temperatures. However, significant differences were observed only at 8 °C, between specimens under 500 µmol photons m^{-2} s^{-1} compared to initial control and specimens under 50 µmol photons m^{-2} s^{-1} (Supplementary Tables S2, S4).

The β-car:chl *a* and VAZ:chl *a* ratio did not show significant fluctuations in values, and no significant differences were recorded (Supplementary Tables S2, S4).

The Anthera:chl *a* ratio tends to increase with high light at all temperatures. However, significant differences were observed at 0 and 4 °C, between the 50 and 500 µmol photons m^{-2} s^{-1} treatments after 21 days of cultivation. Significant differences were also observed between temperatures in some treatments (Supplementary Tables S2, S4). Viol:chl *a* presented a trend to decrease in value after 21 days of culture at 50 and 500 µmol photons m^{-2} s^{-1}. In addition, there was a general decrease in values with increasing temperature. Significant differences could be observed between light treatments at 0 °C and between treatments at 0 and 4 °C.

The ratio chl *c2*:chl *a* showed a tendency to increase the values at 500 µmol photons m^{-2} s^{-1}; however, no significant differences were observed for the light factor, while treatments at different temperatures showed significant differences but not a clear pattern (Supplementary Tables S2, S4).

For DPS, an increase with increasing light intensity was observed at 4 and 8 °C. Significant differences between the initial control and 500 µmol photons m^{-2} s^{-1} treatment were recorded at 4 and 8 °C. With respect to the temperature factor, lower values in the initial control treatments at 4 and 8 °C compared to 0 °C were recorded, generating significant differences (Fig. 1f, Supplementary Table S2). The molar ratio (chl *c2*+Fuco)/chl *a* tended to decrease at 0 and 8 °C with high light, while at 4 °C,

values tended to increase. However, no significant differences were observed for the factors light and temperature (Supplementary Tables S2, S4).

Palmaria palmata. Chl *a* tended to increase with increasing light at all temperatures in comparison to the initial control treatment, but this apparent increase was not significant. In addition, no differences were observed between temperatures, although there was a tendency for the concentration to increase with higher temperatures (Fig. 2a, Supplementary Table S2; two-way ANOVA, Tukey HSD, $p < 0.05$). Lut followed the same trend as chl *a*, showing an increase in concentration with high light at 0 and 4 °C, but significant differences between light treatments were only observed at 0 °C. Lut concentrations in the initial control and under 50 µmol photons m^{-2} s^{-1} at 0 °C were significantly lower than at higher temperatures (Fig. 2b, Supplementary Table S2). For β-car, the values tend to decrease at high light at 0 and 8 °C, but no significant differences were observed between light treatments. The opposite can be observed between temperatures. This difference was due to an increase in concentration at higher temperature. Significant differences can be observed between treatments at 0 and 8 °C. (Fig. 2c, Supplementary Table S2).

In terms of phycobilin concentration, Pc showed, in general, a lower concentration than Pe, and significant differences in Pc were observed between initial control and 500 µmol photons m^{-2} s^{-1} treatments at 4 and 8 °C, tending to decrease in concentration with higher light, whereas temperature was not a factor that affected the treatments. For Pe, an increase in concentration at 500 µmol photons m^{-2} s^{-1} treatment was observed at 0 °C.

For temperatures 4 and 8 °C, a decrease in values was observed at high intensity. Significant differences were observed between the initial control and the 500 µmol photons m^{-2} s^{-1} treatments for all temperatures (Fig. 2d–e, Supplementary Table S2).

With respect to Apc, at 0 °C, pigment concentration did not show major variations between the different light treatments. For temperatures 4 and 8 °C, pigment concentration decreased towards the 500 µmol photons m^{-2} s^{-1} treatment. Significant differences were observed between the initial control treatment and the 500 µmol photons m^{-2} s^{-1} treatment for both temperatures. Also, differences were observed between the 50 and 500 µmol photons m^{-2} s^{-1} treatments at 4 °C. With respect to the temperature effect, significant differences were observed between treatments, mainly due to a high concentration in the initial control treatment at 8 °C (Fig. 2f, Supplementary Table S2).

The relative photosynthetic antenna size (Apc+Pc+Pe)/chl *a* is decreased by high irradiance at 4 and 8 °C compared to the initial control treatment and at 50 µmol photons m^{-2} s^{-1} after 21 days of culture (Supplementary Tables S2, S5). Significant differences were observed between the initial control treatment and the 500 µmol photons m^{-2} s^{-1} at 0 and 8 °C. The highest increase in the antennal size was observed at 500 µmol photons m^{-2} s^{-1} at 0 °C. The temperature factor showed significant differences between treatments but did not show a clear trend.

The Pc:chl *a* pigment ratio showed a trend very similar to the antenna size described above. Significant differences were observed between the initial control treatment and
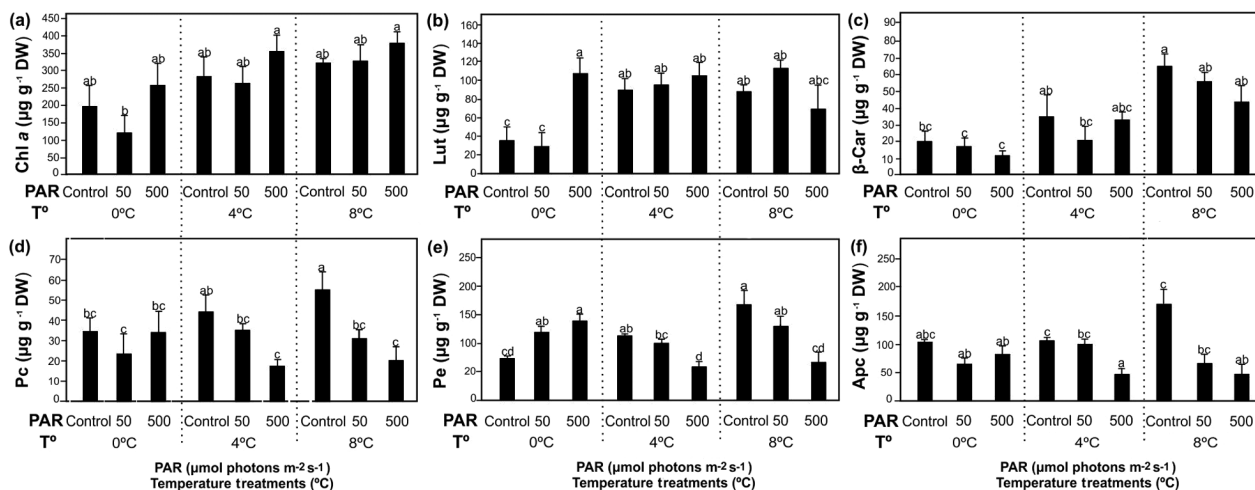

Fig. 2 Mean±SD pigment concentration (*n*=3) in *Palmaria palmata*. For pigments chl *a*, Lut, β-car, Pc, Pe and Apc in (µg g^{-1} DW). Samples at three different temperatures (0, 4 and 8°C) and different light intensities: Control (Initial control measure 50 µmol photons m^{-2} s^{-1}), 50 and 500 µmol photons m^{-2} s^{-1} (after 21 days of culture). Different letters indicate significant differences among light treatments for temperatures (*p* < 0.05).

the 500 µmol photons m^{-2} s^{-1} at 0 and 8 °C (Supplementary Tables S2, S5). The greatest increase in the ratio was observed at 500 µmol photons m^{-2} s^{-1} at 0 °C, while at the same light intensity but at 4 and 8 °C, the pigment ratio tended to decrease. The temperature factor caused significant differences between the 500 µmol photons m^{-2} s^{-1} treatment at 0 and 8 °C; a decrease in the ratio was observed at the highest temperature of 8 °C. The Pe:chl a pigment ratio tended to be influenced by high irradiance after 21 days of culture at 0 °C. While at 8 °C, the values tend to decrease with more light. Significant differences were observed between the initial control and 500 µmol

photons m^{-2} s^{-1} treatment at 0 and 8 °C, while at 4 °C, no differences were observed in the pigment ratio. The temperature factor did not show significant differences between treatments (Supplementary Tables S2, S5). Finally, for the Apc:chl a pigment ratio, an increase in values could be observed for the 500 µmol photons m^{-2} s^{-1} treatment at 0 °C. Significant differences were recorded between the initial control and the 500 µmol photons m^{-2} s^{-1} treatment. However, the 500 µmol photons m^{-2} s^{-1} treatment showed significant differences between temperatures, caused by a decrease in the pigment ratio at higher temperature after 21 days of culture (Supplementary Tables S2, S5).

Antioxidant activity

The antioxidant activity expressed by the DPPH assay in *D. aculeata* tends to increase at 500 µmol photons m^{-2} s^{-1} at all temperatures. Significant differences between the 500 µmol photons m^{-2} s^{-1} and the initial control and the 50 µmol photons m^{-2} s^{-1} treatment were recorded. Significant differences were observed for the factors light and temperature (Fig. 3a, Supplementary Table S2; two-way ANOVA, Tukey HSD, $p < 0.05$).

In *P. palmata*, an increment in the DPPH activity was detected in high light at 500 µmol photons m^{-2} s^{-1} at 4 °C compared to the low light treatment. At 0 and 8 °C treatments, no major variation in antioxidant activity was observed. Significant differences were observed only for light factor (Fig. 3b, Supplementary Table S2).

Regarding the phlorotannin content in *D. aculeata*, at 0 and 8 °C, the concentration was higher in the treatment at 500 µmol photons m^{-2} s^{-1} after 21 days of cultivation. This was expressed in the presence of significant differences at 500 µmol photons m^{-2} s^{-1} compared to the initial control and the 50 µmol photons m^{-2} s^{-1} treatment. The temperature factor did not show significant differences between treatments (Fig. 3c, Supplementary Table S2).

Discussion

The most critical abiotic driver governing macroalgal global distribution is temperature (Lüning 1990), with direct effects on integrative traits like photosynthetic performance, growth and reproduction (Falkowsi & La Roche 1991). On smaller spatial scales, irradiance is the central but complex abiotic driver controlling the photosynthetic process (Hurd et al. 2014). The composition of the photosynthetic apparatus can be modulated by high irradiance and changes in ambient temperature, and polar macroalgal species are mainly considered to be shade-adapted (Weykam et al. 1996).
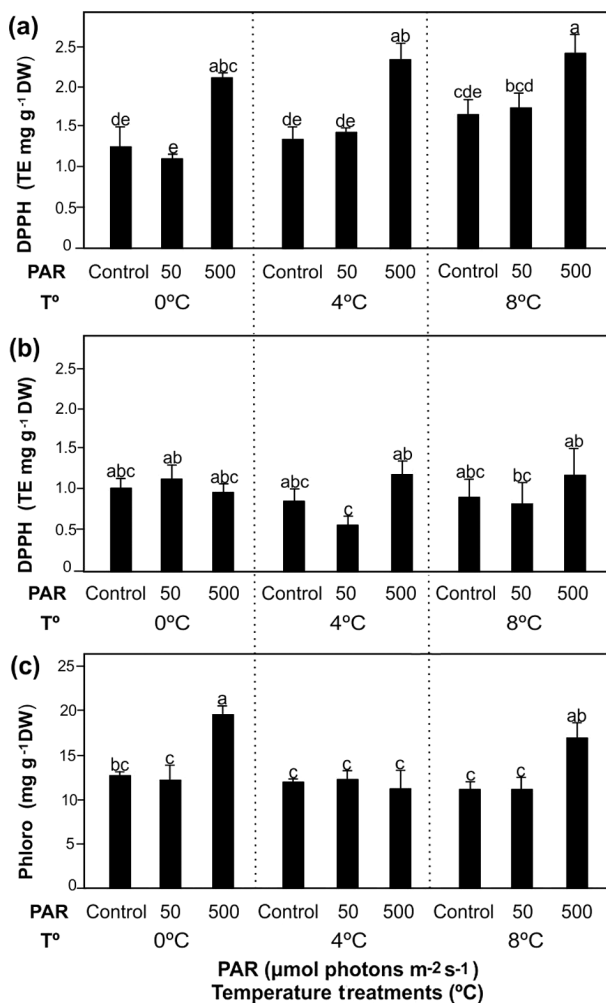

Fig. 3 Antioxidant activity (n=3) is shown for (a) *Desmarestia aculeata* DPPH (TE mg g^{-1} DW) (b) *Palmaria palmata* DPPH (TE mg g^{-1} DW), and (c) *D. aculeata* phlorotannins (mg g^{-1} DW). Samples at three different temperatures (0, 4 and 8°C) and different light intensities: control (initial control measure 50 µmol photons m^{-2} s^{-1}), 50 and 500 µmol photons m^{-2} s^{-1} (after 21 days of culture). Different letters indicate significant differences among treatments ($p < 0.05$).

Both species, *D. aculeata* and *P. palmata*, with a similar cold-temperate to polar distribution, presented overall similar strategies of ecophysiological acclimation patterns to variation in light and temperature conditions. However, in our experiments, each species showed mixed responses to both increased irradiance and temperature.

Photosynthetic performance

In general, *D. aculeata* and *P. palmata* showed similar responses to the experimental variations in irradiance and temperature.

Maximal quantum yield F_v/F_m decreased under high irradiance in both species. The effect of decreased F_v/F_m at high light intensities was also observed in the brown algae *Alaria esculenta* (Bischof et al. 1999) and in ice algae in Nunavut, Canada (Galindo et al. 2017). It is known that high irradiance may cause photoinhibition in macroalgae, particularly in species inhabiting deeper waters (Hanelt 1998; Karsten et al. 2001), such as *D. aculeata* in the subtidal zone. However, *P. palmata* showed a tendency to increase its F_v/F_m values with increasing temperature. The opposite was registered by Gordillo et al. (2016), who observed an overall negative effect of temperature increase on F_v/F_m in different macroalgal lineages in the Arctic. The reversible reduction in maximal quantum yield was characterized by Osmond (1994) as 'dynamic photoinhibition', a strategy to protect photosynthetic reaction centres from the excess light absorbed, and thus to suppress the generation of reactive oxygen. Persistently, low values of F_v/F_m in treatments with high irradiance indicate, according to observations by Lüder et al. (2002), damage to the PSII reaction centre. Dynamic photoinhibition is described as a common strategy of protection against high irradiance in algae inhabiting the intertidal zone (Becker et al. 2009).

Both species studied presented a trend to decrease in rETRmax values at increasing irradiances and in some temperature treatments. However, in long-term studies, for example, comparing seasonal patterns, the opposite trend is usually observed. Bischof et al. (2002) described that for brown macroalgae in Kongsfjorden, how the photosynthetic variables vary according to the presence of sea-ice cover and underwater light availability. Species such as *D. aculeata* and *Saccharina latissima* show an increase in rETRmax values during the months of highest underwater irradiance and absence of sea ice. For *P. palmata*, Hanelt et al. (2003) conducted studies in the Kongsfjorden area and reported increasing rETRmax at higher temperature. Although temperature was not a decisive factor in this parameter, specific differences were observed in the high light treatment between 8 °C and the other temperatures. Hence, light is suggested to be

the predominant factor in generating stress in the species *P. palmata*. Hanelt et al. (2003) described habitat-specific light-acclimation in *P. palmata*, which might become saturated with light above 100 µmol m^{-2} s^{-1}. However, in our study, there was a decrease in rETRmax at high irradiances, and values generally increased at higher temperatures, which could be attributed to a more efficient drain of reduction equivalents consumed in the Calvin cycle at moderately increased temperatures.

The reduced photosynthetic activity observed in both species during our experiments seems to be a sign of efficient regulatory processes that buffer against rapid and sudden variations in environmental factors and ultimately minimize oxidative stress (ROS). The opposite trend of increasing photosynthetic performance with irradiance was observed in seasonal studies, reflecting acclimation processes to a changing light environment over weeks to months (Aguilera et al. 2002; Bischof et al. 2002).

The initial slopes of the P-E curves (i.e., α values) in *D. aculeata* and *P. palmata* showed a similar pattern: decreasing α in the presence of high irradiance at 0 °C. Neither species showed significant effects of temperature for this parameter. This response shows that the two species are similarly able to adapt to individual changes in environmental factors.

In both *D. aculeata* and *P. palmata*, the parameter *E*k tended to decrease in the presence of high irradiance. High irradiance strongly affects *D. aculeata*, which is explained by its characteristic as a subtidal species. Photosynthesis in species from deeper waters is more prone to inhibition in the presence of high irradiance and may take longer to recover (Hanelt 1998; Karsten et al. 2001). Although, in general, light was not the deciding factor for *P. palmata*, temperature made a difference. A different pattern was observed by Sagert & Schubert (2000), who observed an increase in *E*k values with increasing light intensity for *P. palmata*. The inconsistency between our results and those of Sagert & Schubert may lie in the limited duration of our experiment, which may not have been long enough to achieve acclimation to increased irradiances. On the other hand, low *E*k values are a sign of the adaptation to darkness or general light-limitation, as is characteristic for polar algae (Wiencke et al. 2006).

Photosynthetic pigments

Becker et al. (2009) mention that a decrease in temperature, combined with an increase in PAR, is a severe stressor for algae, resulting in the inhibition of photosynthetic performance and alterations in pigment content. Both species studied presented different responses with respect to the combination of abiotic drivers, which

was also reflected by pigment composition changes in the two species.

The species *D. aculeata* presented a decrease in overall pigment concentration, mainly in chl *a*, chl *c2*, Fuco and β-car, mainly in response to increasing irradiance; for Fuco and β-car, temperature was an additional driver. It is well established that this type of physiological adjustment is a key in the process of photo-acclimation under high irradiance (Hurd et al. 2014). In particular, light harvesting is reduced to avoid overexcitation, ROS production and chronic photoinhibition. In seasonal studies of *Laminaria digitata* and *S. latissima*, it has been observed that, like in *D. aculeata*, the high irradiance and the increase in temperature during the summer months influence pigment concentration, which has been reported as acclimation to seasonal changes (Hallerud 2014).

The VAZ pigments participated in the xanthophyll cycle were generally present at low concentrations. The low concentration of these pigments in polar seaweed was also recorded by Hallerud (2014). However, in our study, all three pigments responded to increasing irradiance as the most driving factor. For example, Zeax showed an increase at higher irradiance in all temperatures in *D. aculeata*, this being a short-term regulatory response. Heriyanto et al. (2017) recorded for brown algae that Zeax increases as a consequence of de-epoxidation of Viol in response to high light intensities. This result is further reflected in *D. aculeata* by the increasing trend in the pigment ratio of Fuco:chl *a* and Zeax:chl *a* at high light. Overall, our data show that this species is sensitive to high irradiance, as reflected in the ratios Anthera:chl *a* and Viol:chl *a*. Our experiments also showed that responses to increasing temperature for parameters such as Anthera:chl *a* and Viol:chl *a* are negatively affected, while chl *c2*:chl *a* did not show a clear pattern with respect to temperature.

These findings are consistent with laboratory and field studies carried out by Chapman & Burrows (1970), who showed that light is more important than temperature for the development and growth of *D. aculeata*. On the other hand, pigment ratios, such as β-car:chl *a* and VAZ:chl *a*, and molar ratios were not affected by light or temperature for *D. aculeata* in our study. The trend of increasing pool size of the xanthophyll cycle (VAZ) in the face of high irradiances at 0 and 4 °C reinforces the idea that the light sensitivity of *D. aculeata* is key to its physiology, and that temperature might be a secondary factor, generating the decrease of VAZ. At the same time, we found an increase in DPS in the presence of high irradiances. The increase in VAZ and DPS is part of the process of photoprotection against oxidative stress (Olischläger et al. 2017; Li et al. 2019). For *D. aculeata*, data suggest a strong capacity to acclimate to environmental variables, with

light and temperature being the triggers of physiological adjustments. In our study, *D. aculeata* presented higher values at 0 °C compared to the higher temperatures, in agreement with observations by Bischof et al. (2002), who found that decreases in temperature have modulating effects on these processes.

In *P. palmata*, high concentrations of chl *a* were maintained in all treatments. However, seasonal studies of *P. palmata* showed an increase in chl *a* concentration during the spring months and a subsequent decrease in response to high irradiance during the summer months (Hallerud 2014; Lalegerie et al. 2020). Although our study shows the response over a limited period of time, it indicates well the acclimation capacity of *P. palmata*. However, it is to be expected that increasing irradiance beyond a certain threshold would result in a loss of chl *a*, to avoid photodamage and photoinhibition, as described by Raven & Hurd (2012).

This notion is supported by the increase of β-car to high temperature, and the Lut increment at high irradiance and low temperature observed in this study. However, some studies suggest that in *P. palmata* specimens, in France, carotenoids, in general, function as accessory pigments in light-harvesting and not as a mechanism of photoprotection (Hashimoto et al. 2016: Lalegerie et al. 2020). Still, we suggest that for *P. palmata* at High-Arctic latitudes, carotenoids could have an important role contributing to the mechanisms of photoprotection, particularly in a high irradiance/low temperature environment. This trend was also observed by Hallerud (2014) during a seasonal study of *P. palmata*.

With respect to the red algal pigments, none of the phycobilliproteins showed large differences at low temperatures, but they decreased in concentration at high irradiance. Aguilera et al. (2002) described that *P. palmata* decreases in Pe and Pc under high irradiance. The increase in the antenna size and pigment ratios Pe:chl *a*, Pc:chl *a* and Apc:chl *a* at high irradiance was observed at low temperatures, while the opposite trend was observed with higher temperatures, suggesting the combined effect of both factors in *P. palmata*.

Both species tended to have a combined response to irradiance and temperature variation. *Desmarestia aculeata* commonly inhabits the subtidal zone, but it is also observed shallower areas. *Palmaria palmata* inhabits the intertidal zone, a habitat characterized by great variation in environmental drivers, and is, therefore, expected to be more adapted to tolerating significant increases in irradiance.

Antioxidative activity

A number of macroalgae have the capacity to produce phlorotannins as a general response to different types of

environmental stress, allowing a general but fast adaptive response (Springer et al. 2017). The concentration of phlorotannins in *D. aculeata* was influenced by high irradiance. It is possible that in *D. aculeata*, phlorotannins are mainly found as cell wall compounds, playing a phytoprotective role with respect to environmental variations such as PAR light. However, phlorotannins have several secondary functions, such as UV defence and warding off herbivores (Koivikko et al. 2005; Abdala et al. 2006; Koch et al. 2015).

In *D. aculeata*, we observed an increase in antioxidant activity at higher irradiances and influenced by high temperature. In this case, the antioxidant activity has an important photoprotective function. In contrast, the antioxidant activity of *P. palmata* is influenced mainly at high irradiances. A similar situation occurs with mycosporins in *P. palmata*; Yuan et al. (2009) observed an increase in mycosporin in high UV light.

In response to both environmental factors, *D. aculeata* might be characterized as an alga with moderate acclimation capacity, while *P. palmata* presents a more pronounced light acclimation capacity and is not strongly affected by temperature.

Ecological implications

The Arctic is currently experiencing a number of rapid environmental changes. He et al. (2019) describe how the decrease in sea-ice cover has led to increased absorption of irradiance into the water column due to its darker surface. Hence, the reduction of sea ice will lead to a further increase in ocean temperature (Higgins & Cassano 2009). In parallel, seaweed communities are constantly changing, and their responses to climate change are fundamental to understanding the current and future coastal ecosystems in the High Arctic (Bartsch et al. 2016; Bischof et al. 2019). Arctic species are increasingly exposed to high irradiances for longer periods of time, in addition to rising temperatures and other variations in environmental variables (Lüning 1990; Filbee-Dexter et al. 2019). Species originating in lower latitudes, such as *D. aculeata* and *P. palmata*, have managed to adapt to Arctic conditions; however, they have maintained their adaptive traits for temperate conditions. Both species studied share similar features with respect to geographic distribution and temperature requirements (Lüning 1990). However, *P. palmata* is more tolerant to high temperatures and usually populates a higher shore level than *D. aculeata*. This difference in depth distribution clearly matches the ecophysiological responses observed during this work. Our study demonstrates how Arctic isolates of these two species, which belong to different algal classes and show similar acclimation responses to variations in

environmental factors, which are, however, based on different biochemical processes. With its higher sensitivity to temperature and irradiance changes, *D. aculeata* might be more affected by increasingly ice-free areas. High light exposure could be counteracted, however, by an increased release of turbid meltwater in coastal areas, reducing light availability. In contrast, it is likely that *P. palmata* will soon become much more abundant in fjord systems throughout the Arctic on the account of its relative resistance to temperature increases, as diminishing sea ice will offer the species greater opportunities to populate the shallow subtidal zone.

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Disclosure statement

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