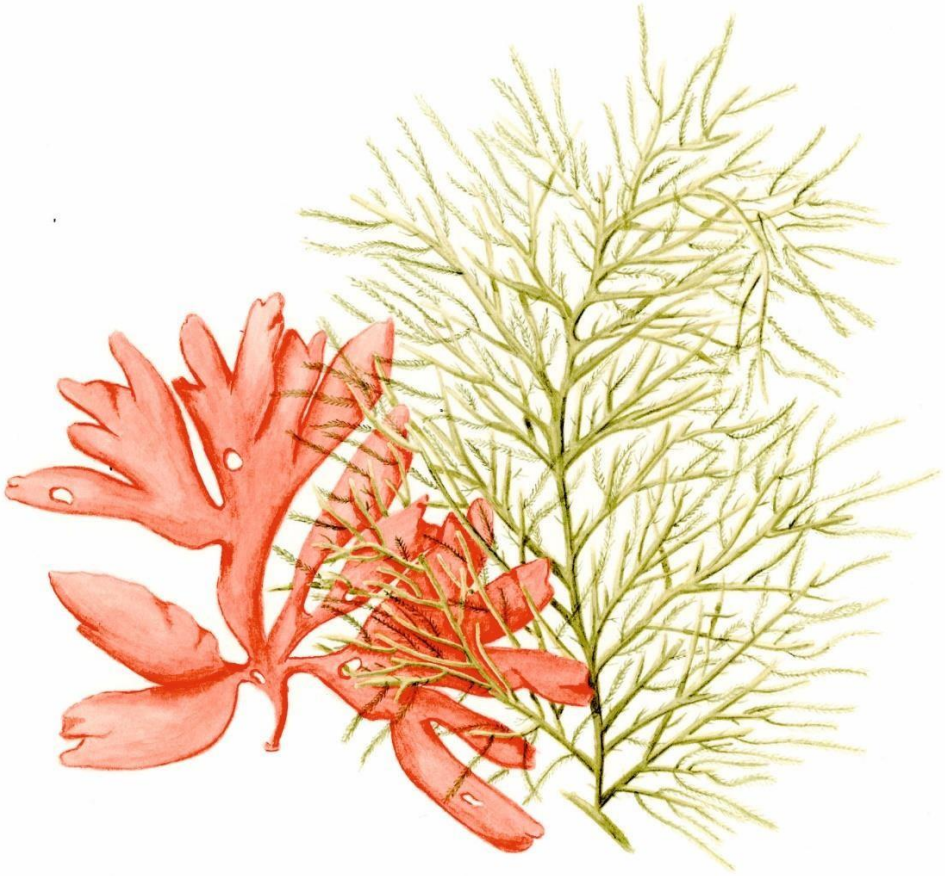
Interactive effects of environmental drivers on boreal-Arctic seaweeds in response to climate change

Dissertation 2022

Johanna Marambio Gallardo



University of Bremen

Department of Marine Botany- Faculty Biology/ Chemistry

Interactive effects of environmental drivers on boreal-Arctic seaweeds in response to climate change

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Johanna Valeska Marambio Gallardo

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I need the sea because it teaches me:
I don't know if I learn music or consciousness:
I don't know if it's only a wave or a deep being
or just hoarse voice or dazzling...

The fact is that even when I am asleep
I somehow magnetically circulate
in the universe of the swell...

What it taught me before I keep it! It is air,
incessant wind, water, and sand...

The Sea, Pablo Neruda, Chile

Ich brauche das Meer, weil es mir Dinge lehrt:
Ich weiß hierbei nicht, ob es sich vielmehr um Musik oder Bewusstsein handelt:
Ich weiß hierbei nicht, ob es sich um eine Welle, ein tiefgründiges Wesen,
eine raue Stimme oder doch um etwas Umwerfendes handelt...

Die Tatsache ist, dass ich bis zum Moment des Einschlafens
auf scheinbar magnetische Art
im Universum des Wellengangs umherkreise.

Und was es mir zuvor gelehrt hat, behalte ich fest bei mir! Luft,
unaufhörlicher Wind, Wasser und Sand…

Das Meer von Pablo Neruda, Chile

Necesito del mar porque me enseña:
no sé si aprendo música o conciencia:
no sé si es ola sola o ser profundo
o sólo ronca voz o deslumbrante…

El hecho es que hasta cuando estoy dormido
de algún modo magnético circulo
en la universidad del oleaje…

¡Lo que antes me enseñó lo guardo! Es aire,
incesante viento, agua y arena…

El Mar, Pablo Neruda, Chile

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Summary

Temperature increase due to climate change is most pronounced in the high latitudes. Due to the process of Arctic Amplification the amplitude of change in a range of environmental drivers is intensified in polar ecosystems. The Svalbard archipelago in the Arctic is no exception, and its fjords have been extensively studied for over 100 years, providing important information on the present and future of Arctic ecosystems in the face of climate change. This archipelago is known to host a great diversity of marine organisms, including seaweeds. As being sessile organisms, seaweeds are constantly exposed to a highly seasonal regime and, in recent decades, are strongly affected by the intensification of abiotic factors due to climate change. In particular, the increase in temperature directly affects both the ecophysiology and the distribution of seaweeds in the Arctic. On the other hand, the effect of the interaction of abiotic factors on Arctic seaweeds still is an underexplored field. In response to environmental change, seaweed show different ranges of acclimation, both on the physiological and biochemical level. While hitherto most studies addressed the keystone engineering species of kelp, other abundant, and hence ecologically relevant, species of seaweed have been understudied. However, in order to address biodiversity shifts in Arctic fjord systems as resultant from environmental change information on physiological tolerance on a wide range of species is indispensable. The aim of this study is to characterize the acclimation mechanisms of the brown alga *Desmarestia aculeata* and the red alga *Palmaria palmata* from an high Arctic fjord system (Kongsfjorden, Svalbard), to changing and interacting environmental drivers.

Acclimation to abiotic factors such as temperature and irradiance were evaluated in *D. aculeata* and *P. palmata* in **publication I**. Both species were collected in Kongsfjorden during summer 2019, and exposed to different temperatures 0, 4 and 8 °C and constant irradiance 50 - 500 µmol photons m^{-2} s^{-1}, for 21 days. The similar geographic distribution of the two species studied also implied a similar acclimation potential. Being a seaweed species that generally grows in the upper subtidal and lower intertidal, *D. aculeata* was highly sensitive to the interaction of irradiance and temperature; while *P. palmata*, being a seaweed that inhabits the intertidal, showed a higher tolerance to constant high irradiance. Even so, the increase in temperature is shown to be an important factor in the physiological and biochemical regulation of both species.

In Arctic fjord systems, an increase in meltwater discharge due to warmer temperatures, melting snow and calving glaciers is observed. Consequently, shallow-water benthic species become frequently exposed to hyposalinity and ice-free conditions.

Tolerance to hyposalinity and the pronounced variation in irradiance over daily cycles were evaluated in *P. palmata* **(Publication II)**. Individuals of this red algal species were collected during the summer of 2019. The samples were cultured at a constant temperature of 0 °C, and under a daily irradiance cycle mimicking Arctic summer conditions and different salinities at S_A 34, 28 and 18 in order to simulate the effects of melt water run-off into fjord systems. Hyposalinity conditions strongly affected the daily photosynthetic regulation of *P. palmata*. The decrease in photosystem II maximum quantum yield (F_v/F_m) and a low non-photochemical quenching of chlorophyll fluorescence (NPQ) at the end of the experiment show a decrease in the responsiveness of *P. palmata* to variations in daily irradiance under hyposalinity conditions. Apparently, *P. palmata* at high latitudes only has a limited ability to acclimate to low salinity, as indicated by photosynthetic damage and finally pigment degradation. Consequently, increased hyposaline conditions caused by meltwater run-off into Arctic fjords might result into the migration of *P. palmata* to deeper waters or areas with higher salinities, as *e.g.,* open coasts of the Svalbard Archipelago.

The effect of meltwater and the interaction of hyposalinity and irradiance was also studied in the brown seaweed *D. aculeata* in **publication III**. The controlled hyposalinity conditions to which *D. aculeata* was exposed to did not promote physiological and biochemical damage to the samples. However, although this population can inhabit the intertidal zone, high irradiance may still be a controlling factor in this species. This is because *D. aculeata* showed some variation in measured parameters during high and low irradiance, a possible sign of light stress.

In conclusion, this work provides important information on the acclimation process of species with similar boreal - Arctic distribution, *D. aculeata* and *P. palmata*. Both species were exposed to environmental factors (temperature, irradiance and salinity), which have been intensifying in recent decades due to climate change. The species studied respond physiologically and biochemically to environmental variations and the interaction between them. The results obtained during this thesis are a contribution to the understanding of the current and future situation of the Arctic marine flora in presence of climate change.

Zusammenfassung

Der durch den Klimawandel bedingte Temperaturanstieg zeigt sich am deutlichsten in den hohen Breitengraden. Aufgrund des Prozesses der arktischen Verstärkung (Arctic Amplification) ist die Amplitude der Veränderungen einer Reihe von Umweltfaktoren in polaren Ökosystemen am stärksten ausgeprägt. Die Inselgruppe von Spitzbergen in der hohen Arktis bildet hier keine Ausnahme. Ihre Fjorde werden seit über 100 Jahren eingehend untersucht und lieferten bereits wichtige Erkenntnisse über die Gegenwart und Zukunft arktischer Ökosysteme angesichts des Klimawandels. Spitzbergen beherbergt eine große Diversität mariner Organismen, darunter auch Großalgen. Da es sich hierbei um sessile Organismen handelt, sind sie ständig starken jahreszeitlichen Schwankungen ausgesetzt und in den letzten Jahrzehnten stark von der Veränderung der abiotischen Faktoren aufgrund des Klimawandels betroffen. Insbesondere der Temperaturanstieg wirkt sich direkt auf die Ökophysiologie und die Verbreitung von Algen in der Arktis aus. Andererseits sind die Auswirkungen des Zusammenspiels abiotischer Faktoren auf die arktischen Algen noch immer ein wenig erforschtes Gebiet. Als Reaktion auf Umweltveränderungen zeigen Algen unterschiedliche Anpassungen, sowohl auf physiologischer als auch auf biochemischer Ebene. Während sich die meisten Studien bisher mit den habitat-bildenden Brauntangen ("kelps") befassten, wurden andere häufig vorkommende und daher ökologisch relevante Algenarten noch nicht ausreichend untersucht. Um jedoch die Veränderungen der Artenvielfalt in arktischen Fjordsystemen infolge von Umweltveränderungen zu erfassen, sind Informationen über die physiologische Toleranz einer Vielzahl von Arten unerlässlich. Ziel dieser Studie ist es daher, die Anpassungsmechanismen der Braunalge *Desmarestia aculeata* und der Rotalge *Palmaria palmata* aus einem hocharktischen Fjordsystem (Kongsfjorden, Svalbard) an veränderte und interagierende Umweltfaktoren zu charakterisieren.

Die Akklimatisierung an abiotische Faktoren wie Temperatur und Bestrahlungsstärke wurde bei *D. aculeata* und *P. palmata* in **Publikation I** untersucht. Beide Arten wurden im Sommer 2019 im Kongsfjord, Svalbard, gesammelt und 21 Tage lang verschiedenen Temperaturen von 0, 4 und 8 °C sowie einer konstanten Bestrahlungsstärke von 50 - 500 µmol Photonen m^{-2} s^{-1} ausgesetzt. Die ähnliche geografische Verteilung der beiden untersuchten Arten impliziert auch ein ähnliches Akklimatisierungspotenzial. Da *D. aculeata* eine Algenart ist, die im Allgemeinen im oberen Subtidal und unteren Intertidal wächst, reagierte sie sehr empfindlich auf die Wechselwirkung von Bestrahlungsstärke und Temperatur, während *P. palmata*, eine Algenart, die im Intertidal lebt, eine höhere Toleranz gegenüber konstant hoher Bestrahlungsstärke zeigte.

Dennoch hat sich gezeigt, dass der Temperaturanstieg ein wichtiger Faktor für die physiologische und biochemische Akklimatisation der beiden Arten ist.

In arktischen Fjordsystemen wird ein Anstieg des Schmelzwasserabflusses aufgrund wärmerer Temperaturen, schmelzenden Schnees und kalbender Gletscher beobachtet. Infolgedessen sind die benthischen Arten des Flachwassers häufig einem niedrigen Salzgehalt und eisfreien Bedingungen ausgesetzt.

Die Toleranz gegenüber Hyposalinität und die ausgeprägten Schwankungen der Bestrahlungsstärke im Tagesverlauf wurden bei *P. palmata* untersucht **(Publikation II)**. Individuen dieser Rotalgenart wurden im Sommer 2019 gesammelt. Die Proben wurden bei einer konstanten Temperatur von 0 °C und unter einem täglichen Bestrahlungszyklus kultiviert, der arktische Sommerbedingungen und unterschiedliche Salzgehalte bei S_A 34, 28 und 18 nachahmt, um die Auswirkungen des Schmelzwasserabflusses in Fjordsystemen zu simulieren. Die Hyposalinitätsbedingungen wirkten sich stark auf die tägliche photosynthetische Regulation von *P. palmata* aus. Die Abnahme der maximalen Quantenausbeute des Photosystems II (F_v/F_m) und eine geringe nicht-photochemische Löschung der Chlorophyllfluoreszenz ("non-photochemical quenching" - NPQ) am Ende des Experiments zeigen eine Abnahme der Reaktionsfähigkeit von *P. palmata* auf Schwankungen der täglichen Bestrahlungsstärke unter Hyposalinitätsbedingungen. Offensichtlich ist *P. palmata* in hohen Breitengraden nur begrenzt in der Lage, sich an niedrige Salzgehalte anzupassen, wie die Schädigung der Photosynthese und schließlich der Pigmentabbau zeigen. Folglich könnten verstärkt hyposaline Bedingungen, die durch Schmelzwasserabfluss in arktische Fjorde verursacht werden, zur Abwanderung von *P. palmata* in tiefere Gewässer oder Gebiete mit höheren Salzgehalten führen, wie z. B. die offenen Küsten des Spitzbergen-Archipels.

Die Auswirkung von Schmelzwasser und die Interaktion von Hyposalinität und Bestrahlungsstärke wurde auch an der Braunalge *D. aculeata* in **Publikation III** untersucht. Die kontrollierten Hyposalinitätsbedingungen, denen *D. aculeata* ausgesetzt war, führten nicht zu einer physiologischen und biochemischen Schädigung der Proben. Obwohl *D. aculeata* auch die Gezeitenzone bewohnen kann, kann eine hohe Bestrahlungsstärke dennoch einen begrenzenden Kontrollfaktor für diese Art darstellen. Dies liegt daran, dass *D. aculeata* eine gewisse Variation der gemessenen Parameterwerte bei hoher und niedriger Bestrahlungsstärke zeigte, was ein mögliches Zeichen für Lichtstress ist.

Resumen

El aumento de la temperatura debido al cambio climático es más pronunciado en las latitudes altas. Debido al proceso de amplificación del Ártico, la amplitud del cambio en una serie de factores ambientales se intensifica en los ecosistemas polares. El archipiélago de Svalbard, en el Ártico, no es una excepción, y sus fiordos se han estudiado ampliamente durante más de 100 años, proporcionando información importante sobre el presente y el futuro de los ecosistemas árticos ante el cambio climático. Este archipiélago es conocido por albergar una gran diversidad de organismos marinos, entre ellos las algas. Al ser organismos sésiles, las algas están constantemente expuestas a un régimen altamente estacional y, en las últimas décadas, se ven fuertemente afectadas por la intensificación de los factores abióticos debido al cambio climático. En particular, el aumento de la temperatura afecta directamente tanto a la ecofisiología como a la distribución de las algas en el Ártico. Por otro lado, el efecto de la interacción de los factores abióticos sobre las algas del Ártico sigue siendo un campo poco explorado. En respuesta al cambio medioambiental, las algas muestran diferentes rangos de aclimatación, tanto a nivel fisiológico como bioquímico. Mientras que hasta ahora la mayoría de los estudios se han centrado en especies bioingenieras "kelp", mientras que otras especies de algas abundantes, y por tanto ecológicamente relevantes, han sido escasamente estudiadas. Sin embargo, para abordar los cambios en la biodiversidad de los sistemas de fiordos del Ártico como resultado del cambio medioambiental, es indispensable disponer de información sobre la tolerancia fisiológica de una amplia gama de especies. El objetivo de este estudio es caracterizar los mecanismos de aclimatación del alga parda *Desmarestia aculeata* y el alga roja *Palmaria palmata* presentes en el sistema de fiordos del Ártico superior (Kongsfjorden, Svalbard), expuesta a los factores ambientales cambiantes e interactivos.

Se evaluó la aclimatación a factores abióticos como la temperatura y la irradiación en *D. aculeata* y *P. palmata* en la **publicación I**. Ambas especies fueron colectadas en Kongsfjorden durante el verano de 2019, y expuestas a diferentes temperaturas 0, 4 y 8 °C y a una irradiancia constante de 50 - 500 μmol de fotones m^{-2} s^{-1}, durante 21 días. La distribución geográfica similar de las dos especies estudiadas también implicaba un potencial de aclimatación similar. Al ser una especie de alga que generalmente crece en el submareal superior y en el intermareal inferior, *D. aculeata* fue muy sensible a la interacción entre la irradiancia y la temperatura; mientras que *P. palmata*, al ser un alga que habita en el intermareal, mostró una mayor tolerancia a la irradiancia alta constante. Aún así, el aumento de la temperatura se muestra como un factor importante en la regulación fisiológica y bioquímica de ambas especies.

En los sistemas de fiordos del Ártico se observa un incremento en la descarga de agua de deshielo debido a las temperaturas más cálidas, el derretimiento de la nieve y el desprendimiento de los glaciares. En consecuencia, las especies bentónicas de aguas poco profundas se ven expuestas con frecuencia a la hiposalinidad y a las condiciones de ausencia de hielo.

Se evaluó la tolerancia a la hiposalinidad y la pronunciada variación de la irradiación a lo largo de los ciclos diarios en *P. palmata* **(Publicación II)**. Se colectaron individuos de esta especie durante el verano de 2019. Las muestras se cultivaron a una temperatura constante de 0 °C, bajo un ciclo de irradiancia diario que imitaba las condiciones del verano Ártico y diferentes salinidades a S_A 34, 28 y 18, con el fin de simular los efectos de la escorrentía de agua de deshielo en los sistemas de fiordos. Las condiciones de hiposalinidad afectaron fuertemente a la regulación fotosintética diaria de *P. palmata*. La disminución del rendimiento cuántico máximo del fotosistema II (F_v/F_m) y un bajo apagamiento no fotoquímico de la fluorescencia de la clorofila (NPQ) al final del experimento, muestran una disminución de la capacidad de respuesta de *P. palmata* a las variaciones de la irradiancia diaria en condiciones de hiposalinidad. Aparentemente, *P. palmata* en latitudes altas presenta una capacidad limitada para aclimatarse a condiciones de baja salinidad, como indican los daños fotosintéticos y la degradación pigmentar, observada durante el experimento. En consecuencia, el aumento de las condiciones hiposalinas causado por la escorrentía del agua de deshielo en los fiordos del Ártico podría dar lugar a la migración de *P. palmata* a aguas más profundas o a zonas con salinidades más altas, como, por ejemplo, las costas abiertas del archipiélago de Svalbard.

El efecto del agua de deshielo y la interacción de la hiposalinidad y la irradiación también se estudió en el alga parda *D. aculeata* en la **publicación III**. Las condiciones de hiposalinidad controlada a las que se expuso *D. aculeata* no promovieron daños fisiológicos y bioquímicos en las muestras. Sin embargo, aunque esta población puede habitar la zona del intermareal, la alta irradiancia puede seguir siendo un factor que controla esta especie. Esto se debe, a que *D. aculeata* mostró cierta variación en los parámetros medidos durante la alta y baja irradiancia, siendo un posible signo de estrés lumínico.

En conclusión, este trabajo proporciona información importante sobre el proceso de aclimatación de especies con distribución boreal-ártica similar, *D. aculeata* y *P. palmata*. Ambas especies fueron expuestas a factores ambientales (temperatura, irradiancia y salinidad), factores que se han intensificado en las últimas décadas debido al cambio climático. Las especies estudiadas responden fisiológica y bioquímicamente a las variaciones ambientales y a

la interacción entre ellas. Los resultados obtenidos en esta tesis son una contribución a la comprensión de la situación actual y futura de la flora marina del Ártico en presencia del cambio climático.

List of Abbreviations

AW	Atlantic water
β-Car	β -Carotene
Chl *a*	Chlorophyll a
Chl *c2*	Chlorophyll c2
CO_2	Carbon dioxide
DPPH	2,2-diphenyl-1-picrylhydrazyl
DPS	De-epoxidation state of the xanthophyll cycle
*E*k	Saturation irradiance
Fucox	Fucoxanthin
F_v/F_m	Optimum/Maximum quantum yield of photosystem II
NPQ	Non-photochemical quenching
PAR	Photosynthetically active radiation (400 - 700 nm)
PC	Phycocyanin
PE	Phycoerythrin
pH	Hydrogen potencial
PSII	Photosystem II
rETR	Relative electron transport rate
rETRmax	Maximum relative electron transport rate
ROS	Reactive oxygen species
UV	Ultraviolet radiation
UV-B	Ultraviolet B (280 - 320 nm)
VAZ	Xanthophyll pigment pool
WSC	West Spitsbergen current
Zeax	Zeaxanthin

List of Units

º	degree
ºC	Degree Celsius
µmol	micromole
cm	centimetre
h	hour
km	kilometre
m	metre
mm	milimetre
m/s	Metre/second
S_A	Absolute salinity

1. General Introduction

1.1 *Arctic ecosystems in the face of climate change*

The fascination with Arctic exploration began at the end of the 19th century in 1882 - 1883 with the celebration of the first international polar year, and the Fram expedition between 1893 - 1896 initiated the first scientific research in the region (Barry & Hall McKim 2018). Scientific research in the Arctic region has significantly increased in recent decades to explore the impacts of climate change. Stocker et al. (2013) describe how the Arctic region is one of the areas most affected by rising temperatures in the last years.

Studies in the Svalbard Archipelago, Arctic, indicate that during the summer and winter seasons the temperature has increased between 0.35 and 1.58 °C per decade since 1971, a clear indication of global warming (Adakudlu et al. 2019). The temperature increase in Svalbard has had several consequences: increased glacier retreat and thus increased meltwater runoff (Van Pelt & Kohler 2015), melting of permafrost, and coastal erosion (Rachold et al. 2004). On the other hand, directly in the water, we observe heating of surface waters, an increase in ice-free zones and thus an increased penetration of UV radiation and PAR into the water column (Rahman 2017; Scherrer et al. 2018; Serreze & Meier 2018; Adakudlu et al. 2019). In addition to this, increased coastal sedimentation, intense desiccation processes for the high temperatures in the interdital zone, and decreased salinity in the water column due to snowmelt, leading to hyposalinity conditions in fjords have been reported (Svendsen et al. 2002; Hawkins et al. 2008; Jones et al. 2009).

From the 1980s onwards, in the Sorkappand area of Svalbard, the first changes in biota due to climate change were observed (Weslawski et al. 2010). Therefore, the species that are unable to physiologically acclimate or evolve genetically to the increase in temperature will have to move northwards in search of colder waters (Thomas 2010; Molinos et al. 2015), thus generating a redistribution of organisms (Hastings et al. 2020). Southward et al. (1995) describe how pelagic organisms are expected to redistribute northwards, up to 200-400 miles, and benthic organisms, such as seaweeds, are expected to seek colder waters to the north; for example, the genus *Alaria* is expected to reduce its southern limit, disappearing from the French-British coast, and increase its northern limit in the Arctic. Among the drivers described

above, increasing water temperature is one of the critical factors affecting species composition of the Svalbard Archipelago (Cheung et al. 2009).

1.2 *Kongsfjorden a "natural laboratory" in the Svalbard Archipelago*

The Svalbard archipelago (78.9 ºN; 11.9 ºE) (Fig. 1a) is formed by numerous islands and fjords. Kongsfjorden (79 ºN, 12 ºE) (Fig. 1b) is located on the west coast of Svalbard (Bischof et al. 2019). This fjord is influenced by the Atlantic Water (AW), which circulates through the West Spitsbergen Current (WSC), which may carry a high amount of heat to the Arctic Ocean through the Fram Strait (Schauber et al. 2004). Kongsfjorden is characterised by a length of 20 km, while the width ranges from 4 to 10 km (Svendsen et al. 2002). This fjord is characterised by a shallow, flat water inlet, facilitating water inflow from the outside (Prominska et al. 2018). A series of tidewater glaciers are present both at the fjord's end and towards its eastern shore (Svendsen et al. 2002). These glaciers are one of the main freshwater sources in Kongsfjorden (Weslawski et al. 1995), discharging to the fjord via glacial outflow channels (Prominska et al. 2018). This discharge increases nutrient availability and sediment load in the water column, generating transient hyposaline conditions in the fjord system (Prominska et al. 2018; Diehl 2021).

However, the process of climate change is ongoing, and its effects are expected to increase over time. Currently, changes in the physical and chemical environment of Kongsfjorden include: a reduction of the sea ice cover in winter, leading to a variation in the salinity regime (Hegseth & Sundfjord 2008), ocean acidification due to a decrease in water pH (Leu et al. 2016) and increased exposure to UV-B (Hanelt et al. 2001). Benthic organisms are directly affected by climate change and the associated changes in the coastal-marine environment. In this context, benthic organisms, which inhabit Kongsfjorden, have been studied for a long time because of their high responsiveness to environmental variations due to climate change (Hop et al. 2002).

As a consequence of climate change, there has been an increase in ice-free areas in the Arctic. The presence of this ice-free areas, has a direct effect on organisms due to an increase in wind speed (from 12.0 m/s to 14.2 m/s) and thus an increase in wave intensity from 2.3 m to 3.1 m (Waseda et al. 2018). The marine communities, can respond dynamically to current environmental changes, despite the oceanographic characteristics of the site and the detected anthropogenic emissions governing the Kongsfjorden system (Bischof et al. 2019).

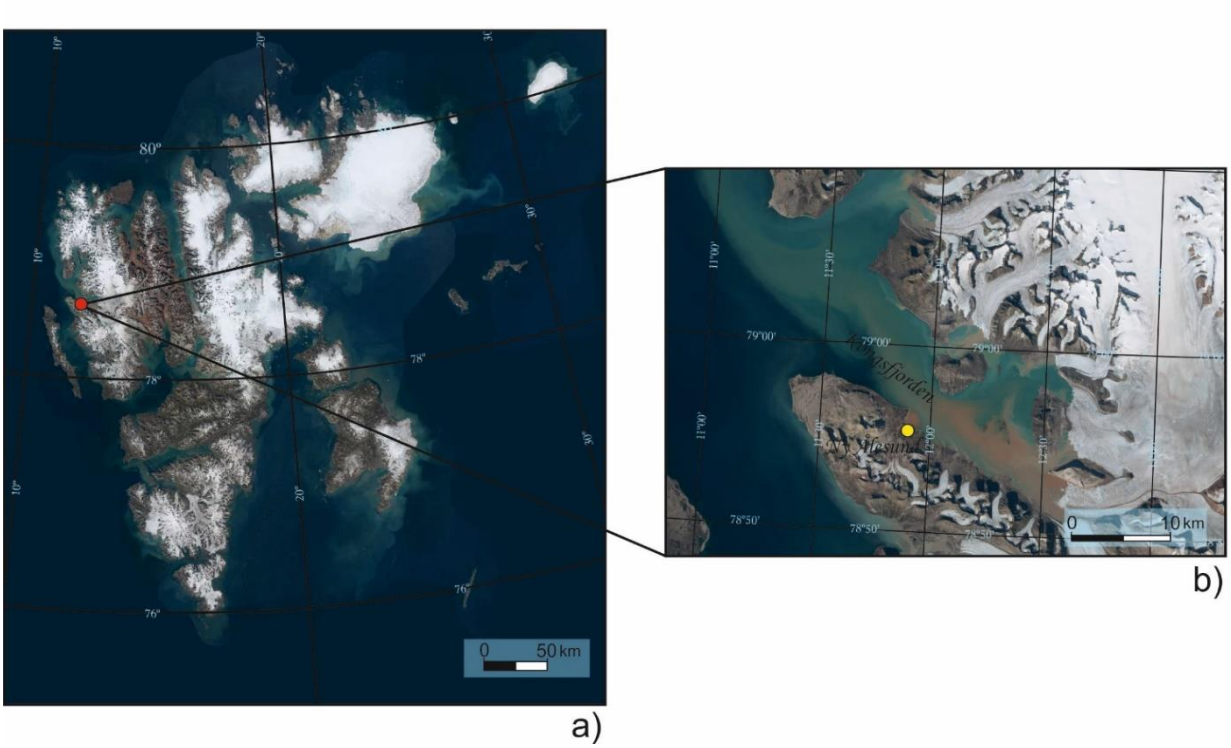

Fig. 1 Map of the Svalbard Archipelago (78.9 ºN; 11.9 ºE), Arctic. a) Svalbard Archipelago, Arctic, red point shows Kongsfjorden; b) Kongsfjorden, yellow point shows the international research and monitoring station Ny Ålesund (78.55 ºN; 11.54 ºE), where most of the scientific research in Svalbard, Arctic, is concentrated. Map retrieved from © TopoSvalbard - Norwegian Polar Institute.

In general, polar systems, especially the high Arctic, are a region sensitive to the impacts of global climate change, which are intensely manifested in the region (Larsen et al. 2014). Kongsfjorden, Svalbard, is not the exception, the ecosystems of this fjord have been studied for more than 100 years, and due to the high number of investigations that have been carried out there, the effects of climate change that have occurred in recent decades have been exposed (Bischof et al. 2019). These characteristics make this fjord a natural laboratory and local indicator of global warming in the Arctic region (Wiencke & Hop 2016).

1.3 *"Seaweeds" are key organisms in the Arctic coastal environment*

Seaweeds have been studied for a long time, specifically in the Svalbard archipelago, starting with the first work by Sommerfelt (1832), and since then descriptive, ecological, and applied

science studies have been ever increasing. After about a century of studies, 197 seaweed species have been described for the Arctic zone, of which 57 are Chlorophyta, 76 Ochrophyta, and 70 Rhodophyta (Fredriksen et al. 2019).

Due to their evolutionary history, the Arctic algal flora is regarded an extension of cold-tolerant temperate species, not giving rise to the notion of Arctic endemism (Bringloe et al. 2020). The endemism theory in the Arctic is mainly based on studies of the origin of kelp forests, which mainly originate from refugia in southern Europe after the last glacial maximum, and eventually distributed to the north (Dunton 1992; Saunders & McDevid 2013). However, the notion of Arctic endemism has been revived, as current genetic studies have revealed Arctic cryptic diversity (Saunders & McDevid 2013; Laughinghouse et al. 2015). On the other hand, the Arctic region has low biodiversity of organisms compared to other regions of the world (Starmans et al. 1999). The high presence of soft substrate resultant from high glacial sedimentation is one of the main reasons facilitating habitat for organisms specialising in soft bottoms (Wlodarska-Kowalczuk et al. 1998; Lippert et al. 2001). However, it has also been observed that in shallower areas between 5 and 15 m, high algal biomass can be found, depending on the type of soft substrate on the seafloor (Wiencke & Hop 2016) (Fig. 2a).
An increase in seaweed biomass has been observed in recent decades in the Arctic region (Krause-Jensen et al. 2021). Bartsch et al. (2015) describe how the *Laminaria digitata* population inhabiting Kongsfjorden has shown an increase in biomass when comparing the periods 1996/1998 with 2012/2013. Another species that increased in abundance is the brown seaweed *Alaria esculenta* which grows during the high-temperature period but consequently loses abundant biomass in autumn (Buschholz & Wiencke 2015). This abundant detached biomass generates effects on the structure and function of the communities living on the soft bottom (Wiencke & Hop 2016; Díaz et al. 2021). In contrary, the brown seaweed *Saccharina latissima* decreases its growth rate and photosynthetic parameter in the presence of high temperature and low salinity F_v/F_m (Baral 2020; Li et al. 2020). Despite the effect of climate change, Arctic seaweed actively participate in the carbon fixation cycle, regulated mainly by Arctic seasonality. In the cold season, an increase in biomass has been recorded, while in the warm season, seaweeds actively fix available carbon (Wiencke et a. 2011), being fundamental in carbon fixation at the regional level (Hop et al. 2012; Iñiguez et al. 2015).

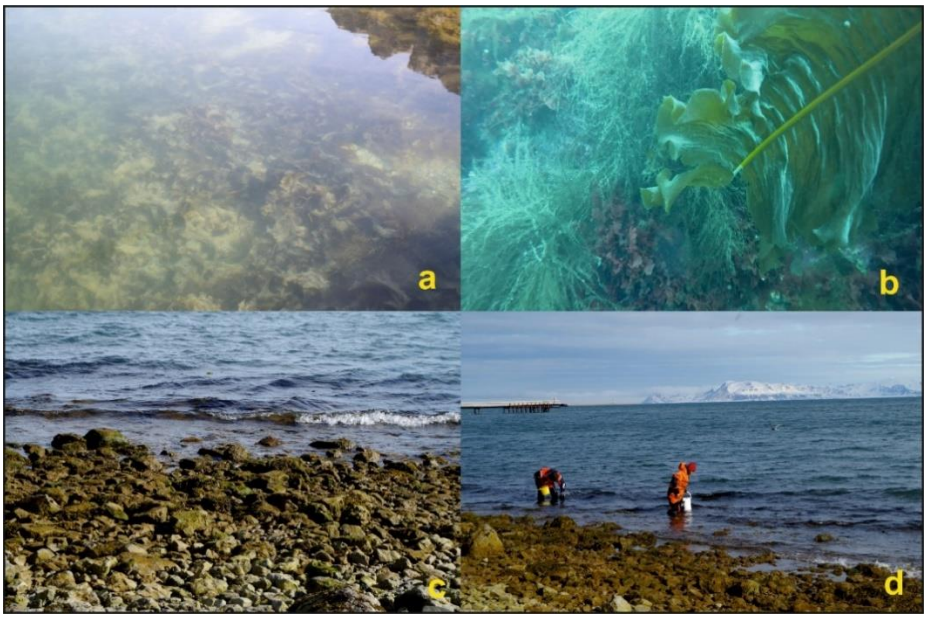

Fig. 2 Subtidal and intertidal zones of Kongsfjorden, Arctic. a) sedimentary bottom at Ny Ålesund (78° 55' N; 11° 55' E); b) Subtidal at Brandal point (78 °56' N; 11° 51' E) *Desmarestia aculeata* collection site, © Sarina Niedzwiedz; c, d) Intertidal rocky shore of Ny Ålesund, collection site of *Palmaria palmata*. © Nora Diehl.

Despite the effect of climate change, Arctic seaweed actively participate in the carbon fixation cycle, regulated mainly by Arctic seasonality. In the cold season, an increase in biomass has been recorded, while in the warm season, seaweeds actively fix available carbon (Wiencke et a. 2011), being fundamental in carbon fixation at the regional level (Hop et al. 2012; Iñiguez et al. 2015).

Seaweed have a fundamental role in providing ecosystem and economic services to the ecosystem (Lippert et al. 2001; Wiencke et al. 2014), such as food, shelter, and habitat (Ware et al. 2019), as well as fulfilling their role as primary producers (Bringloe et al. 2020). Seaweeds have thus positioned themselves as the major structural component of shallow water ecosystems in the Arctic (Seed & O' Connor 1981). But, not all Arctic seaweed species generate large "underwater forest"; many species are associated with the understorey, forming belts as is the case of the species *Desmarestia aculeata* (Hop et al. 2012) (Fig. 2b). Others can inhabit the intertidal and the upper subtidal (Fig. 2c, d), such as the red seaweed *Palmaria palmata*, a species of high economic value due to its versatility, which is currently harvested

and cultivated in the North Atlantic, while natural meadows are conserved in the Arctic region.

Finally, the structure and abundance of seaweed populations are key to preserving ecological functions and maintaining community integrity (Ware et al. 2019).

1.4 *Environmental factors affecting polar seaweeds*

The life history of organisms is marked by diverse interactions between abiotic and biotic environmental factors (Hurd et al. 2014). Lalegerie et al. (2020) describe how intertidal seaweeds are exposed to abiotic factors that fluctuate during the day, such as: seasonality, tide, desiccation, temperature, and photoperiod. On the other hand, depending on where they live, certain seaweeds must deal with the level of hydrodynamics given by tidal cycles, ocean currents, wave actions, and others (Hurd et al. 2014). Seaweeds are currently strongly affected by environmental variations due to climate change, which intensifies abiotic factors such as temperature, salinity, and irradiance (Karsten et al. 2007; Gómez et al. 2011). In this context, specific drivers can have positive or negative effects on organisms, in some cases, their interaction leads to cross-acclimatisation to abiotic factors (Springer et al. 2017; Fernández et al. 2020). On the other hand, it is worth noting that the interactive effects of multiple factors are little studied in seaweeds and that the interaction of drivers at the ecological level is key to understanding the life history of seaweeds (Mineur et al. 2015, Diehl et al. 2020; Monteiro et al. 2021).

1.4.1 *Impact of temperature on seaweeds*

The Arctic region has been characterised by a dynamic climatic history, which has been marked by a series of glacial processes (Miller et al. 2009).

However, this region has recently been strongly affected by the global warming process, warming at twice the global rate (Walsh 2014; He et al. 2019). The increase in air temperature due to the accumulation of greenhouse gases in the atmosphere also contributes to the Arctic warming process (Fyfe et al. 2013). On the other hand, Dai et al. (2019), describe that the amplification process is mainly caused by the decrease in sea ice cover, as a consequence, the water releases more heat into the atmosphere. As a result, there is a positive feedback between

warming and melting of sea ice. Ocean temperatures have increased between 2011 - 2020 by (0.88 [0.68 to 1.01] ºC) compared to the period 1850-1900 (IPCC 2021). These temperature changes have resulted in a decrease in Arctic sea ice cover and, hence, an increase in ice-free waters, leading to changes in coastal benthic zonation and Arctic primary productivity (Gutt 2001; Clark et al. 2013).

Arctic fjords are considered important in thermal regulation of the Svalbard archipelago, as they are the interface between sea and land (Prominska et al. 2018). Kongsfjorden in Svalbard is affected by rising temperatures due to global and local factors. A crucial local factor is the presence of AW, which has generated warming periods ranging from 1990 - 1994, 2001 - 2003, 2006 - 2008, and 2012 - 2013 (Dalpadado et al. 2015; Bloshkina et al. 2021). These warming periods have a clear upward trend in amplitude, frequency and duration, reaching up to 5-6 °C in the surface layers of the water column during the summer season (Hanelt et al. 2004; Tverberg et al. 2019).

The Arctic coast is inhabited by a variety of marine organisms that are affected by temperature increase. Some organisms, such as seaweeds, have in recent years shown a: rapid response, accelerated colonisation, and increased growth rate due to the increase in temperature and the effects it has on the environment, *e.g*., increment of the ice-free zones (Gómez et al. 2011; Quartino et al. 2020).

Temperature is the main abiotic factor governing the biology of organisms, especially seaweeds. This factor is responsable for the regulation of metabolism, reproduction and biogeographical dispersal of algal species (Fredersdorf et al. 2009). However, seaweeds are able to acclimatise or adapt to different temperatures (Hanelt et al. 2003). Acclimatisation to temperature is obtained within days or weeks, whereas adaptation is a process that takes an extended period of time (Davison et al. 1991). It has been observed that the brown seaweed order of Desmarestiales are able to benefit from temperature increases above 5 °C (Gómez et al. 2011). In seaweed (as other primary producers), the central metabolic process is photosynthesis, which is directly dependent on temperature (Hanelt et al. 2003). In some brown algae such as *Alaria esculenta* or *Saccharina latissima*, efficient ecophysiological with the increased of temperature has been observed due to their temperate-arctic distribution, but the photosynthetic process is affected, showing a decrease in F_v/F_m (Roleda 2009). Local extinction events in seaweeds species due to increasing temperature have been described for New Zealand (Bennett et al. 2015; Thomsen et al. 2019). One example is the species *Desmarestia poha*, which has been affected by increasing temperatures in coastal reef water

masses, causing the algae to redistribute 200 km south of its northern limit (Fraser et al. 2012).

The local extinction event occurred off the coast of New Zealand (sub-Antarctic region), but such processes can occur all over the world, mainly in polar regions. However, the effect of temperature on seaweeds and their internal photosynthetic apparatus will depend on the intensity and time of exposure to this condition, and the capacity of acclimation of the species.

1.4.2 *Impact of salinity on seaweeds*

Lalegerie et al. (2020) describe how the differences in salinity concentration in marine habitats depends on space and time, *e.g.,* ocean, salt marshes, estuary, intertidal or subtidal zone, seasonality, tide (tide pools), weather conditions (rainfall). Again, an important driver is global climate change and how this leads to fluctuations in abiotic environmental factors. The Arctic is no exception, and over the years, an increase in meltwater from glaciers in the fjords of the coastal Arctic has been observed, with drainage increasing with each summer (Svendsen et al. 2002; Hanna et al. 2008).

In Arctic fjords like Kongsfjorden, it is possible to observe how glacial runoff affects fjord hydrography and biogeochemistry (Schellenberger et al. 2015). Glacier runoff produces seasonal low salinity pulses (Fig. 3a), causing the surface layers of the water column to receive the most significant load of freshwater (Svendsen et al. 2002). The hyposaline surface layer (Fig. 3b) tends to thicken as it enters the fjord producing a spatial gradient of temperature and salinity within the fjord (Prominska et al. 2018). The hyposaline layer can reach down to 20 m depth, mainly due to periods of wind or wave mixing (Hanelt et al. 2001). Therefore, this hyposaline layer may affect the organisms living in shallow waters. Among the organisms that are affected in the fjord are the seaweeds; this group has representatives that inhabit the intertidal zone and are characterised by being euryhaline, while those that inhabit the subtidal zone are usually stenohaline (Lalegerie et al. 2020). Hence, some species of seaweeds may be more affected by hyposalinity than others based on their respective tolerance levels.

In general, seaweed can respond to osmotic shock by internally regulating ion concentration, synthesizing low-weight molecules (which are concentrated in vacuoles located in the

cytoplasm), and rapidly exchanging with the surrounding water to balance the internal osmotic pressure (Karsten et al. 2007).

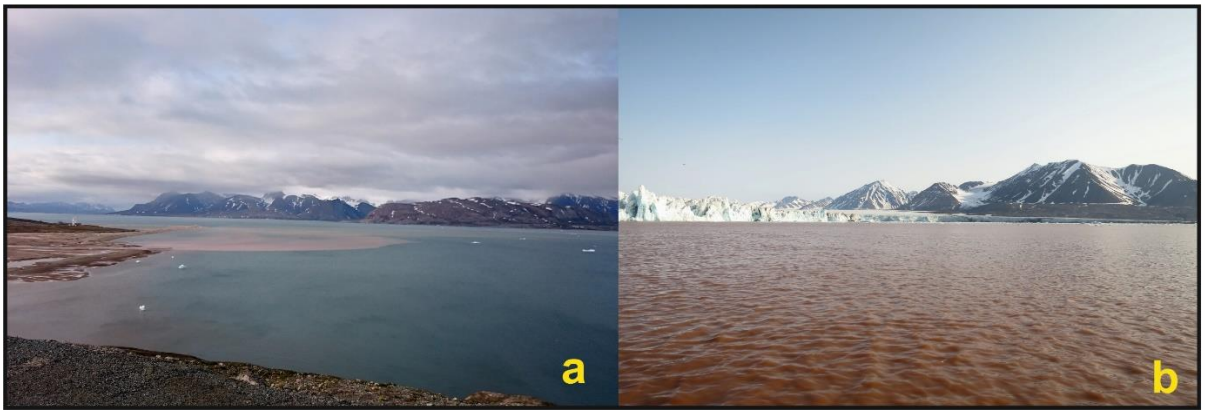

Fig. 3 Photographs of Kongsfjoden, Arctic © Laura Eickelmann. a) Brandal point, with the presence of glacial meltwater; b) glacier area and the surface layer of the water column with meltwater presence.

Therefore, "osmotic acclimation" as a response to salinity fluctuations is relevant and is becoming the main tolerance mechanism to maintain intracellular homeostasis (Kirst 1990). The tolerance mechanism is vital for the survival of Arctic seaweeds in the face of increasingly frequent salinity fluctuations due to climate change.

1.4.3 *Impact of light on seaweeds*

The polar regions are characterised by a pronounced seasonal light cycle (Fig. 4a), with 24 h of darkness during winter and 24 h of light during summer, reaching its peak during mid-summer (May, June, and July) (Pavlov et al. 2019). Half of the solar energy reaching the atmosphere during summer is visible radiation, while the remainder is small fractions of ultraviolet and infrared light (Light et al. 2008). However, the amount and spectral composition of the light reaching the upper part of the water column is critical and is affected by the variability in cloud cover (Maturilli et al. 2019) and by the coverage of sea ice with snow (Pavlova et al. 2019).

Kongsfjorden is characterised by a complex and dynamic underwater light climate, mainly due

to the processes of sea ice formation and melting, the input of local runoff water, and phytoplankton blooms (Hanelt et al. 200; Svendsen et al. 2002). This variability in the underwater light climate of Kongsfjorden directly affects photosynthesizing organisms such as seaweed. Light energy is one of the main abiotic factors affecting the growth and development of these organisms (Lüning 1990). However, it is important to distinguish between the photoperiod to which seaweeds are exposed to and the total irradiance received, both characteristics are governed by seasonality (Hurd et al. 2014). To adjust to the pronounced seasonal light climate some seaweed species apply the strategy of "season anticipators," *e.g., Laminaria solindungula*, this species can grow during the dark months to be in optimal physiological conditions for the months with high irradiance (Kain 1989; tom Dieck 1991). On the other hand, organisms are categorised as "season responders," an example being the species *Saccharina latissima* and *Laminaria digitata*, which response to seasonal light conditions (Wiencke et al. 2009). Local coastal conditions are crucial for understanding the effect of light on algae. In the intertidal, organisms have been recorded to be exposed to high light intensity at low tide, reaching up to 1300 µmol photons m^{-2} s^{-1} in Kongsfjorden, Arctic, during mid-summer (Bischof et al. 1998; Pavlov et al. 2019).

On the other hand, in the subtidal zone, some brown seaweeds present in Kongsfjorden, such as *Desmarestia aculeata* or the so called "kelps," *e.g., Laminaria digitata*, act as natural light barriers against photosynthetically active radiation (PAR) (Fig. 4b), due to the canopy they form (Hanelt et al. 2003). The canopy of these seaweeds can decrease the incident photon irradiance and generate changes in the light quality (Salles et al. 1996); as a result, green and far-red light are present under the seaweed canopy (Salles et al. 1996; Hanelt et al. 2003).

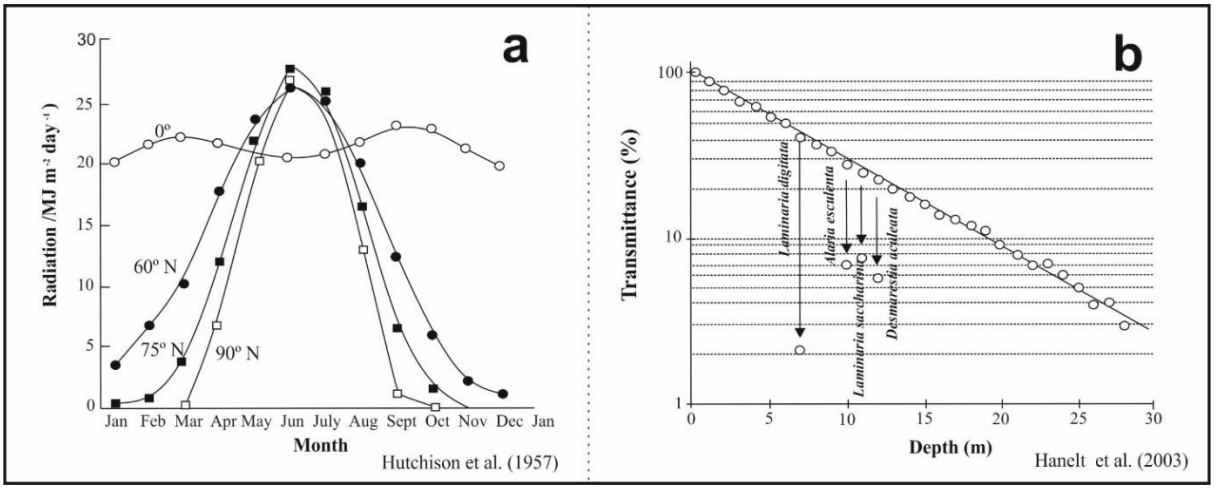

Fig. 4 Annual irradiance data, at sea level data and how the brown seaweeds canopy attenuates this irradiance. a) Monthly estimate of direct radiation (measured at sea level, with corrections

for atmospheric turbidity) on the 15th of each month at northern latitudes; b) Attenuation of photosynthetically active radiation (PAR) by a brown seaweed canopy in the water column, Kongsfjorden, Arctic.

Each seaweed class generally has different light absorption characteristics (Larkum et al. 2003). In deep waters, for example, seaweeds with red pigments (phycobiliproteins) predominate due to the presence of blue-green light (Biebl 1962), but it is also possible to find some brown seaweeds, as they are highly adapted to low light (Lüning 1990). The seaweeds found in the shallower areas or in the intertidal are confronted with high daily irradiance rates. As a result, the internal photosynthetic mechanism of the seaweeds is photoinhibited due to the excess of photons received and photo-oxidation (*e.g.*, photosynthetic pigments and proteins), generated for the formation of reactive oxygen species (ROS) (Mallick & Mohn 2000). However, the effect of irradiance on seaweed is associated with thickness, absorbance, area/weight ratio and size, all associated with light use and its distribution at depth (Gomez & Huovinen 2011). In general, the seaweeds have a high field of action against the incidence of the light factor, which will depend directly on the intrinsic and extrinsic characteristics of the species or individual.

1.5 *Sensors of changes in seaweed ecophysiology*

Seaweeds thrive under constant variation of biotic and abiotic drivers, yet they can apply a wide range of strategies and metabolites to adjust the processes of photosynthesis, respiration, growth or reproduction (Stengel et al. 2011). Among these are photosynthetic, photoprotective, osmoregulatory, antioxidant, antifouling, and other compounds synthesized in response to different types of stresses or in combination (Lalegerie et al. 2020).

Being exposed to strong irradiance pulses, it has been observed how seaweeds may adjust photosynthetic processes, *i.e.* by reallocation of excitation energy into an increased fluorescence signal, heat dissipation induced by non-photochemical quenching (NPQ) and, consequently, a decrease in the maximum quantum yield (F_v/F_m) (Hanelt et al. 2003). By these functions, high irradiance and thus excess photons can cause the PSII to photoinactivate

due to the process of dynamic photoinhibition to decrease the excess energy in the photochemical system (Osmond 1994).

On the other hand, the pigments in seaweeds, are highly sensitive to light, and in the presence of high irradiance, seaweeds are able to regulate their pigment content and composition depending on the situation (Hanelt et al. 2003; Hurd et al. 2014). However, abiotic factors, such as temperature, affect the pigments; increasing temperature is positively correlated with higher pigment content, density in the PSII reaction centers, and increased fucoxanthin - Chl *a* - *c* protein complex, this produces an increased absorption of light (Davison et al. 1991; Machaleck & Davison 1992). On the other hand, red seaweeds are characterised for its accessory pigments called: phycobiliproteins (phycocyanin, phycoerythrin and allophycocyanin) (Hurd et al. 2014). These pigments capable of capturing the energy and transferring it to the photosynthetic process are highly photosensitive (Gantt & Conti 1966; Glazer 1989). Other pigments, such as carotenoids play an essential role in protecting the reaction centers and secondarily as light energy scavengers (Hurd et al. 2014). In red seaweed, it has been observed that their carotenoid pattern is quite simple, with β-Carotene and zeaxanthin, although the latter is commonly substituted by lutein in some groups (Marquardt & Hanelt 2004; Takaichi et al. 2016). Some organisms, such as those belonging to the "brown algae" group, have a more complex carotenoid composition (Dautermann & Lohr 2017). Brown and green algae are able to inter-convert carotenoids from violaxanthin to anteraxanthin and then zeaxanthin (xanthophyll cycle). The activity of this cycle can be quantified by the parameter DPS- de-epoxidation state of the xanthophyll cycle, which is activated to dissipate excess energy in the photosynthetic process (Goss & Jakob 2010; Dautermann & Lohr 2017). As an indicator of emerging stress, like high irradiance, some algal species react by generating ROS - reactive oxygen species, ultimately generating intracellular stress in the organism (Dring 2005). The generation of ROS, promotes the non-photochemical quenching of excited chlorophyll molecules in photosystems or light-harvesting complexes (Ruban 2016). In reponse to ROS generation, algae, mainly brown seaweeds, are able to generate phlorotannins, which act as antioxidants, mainly protecting photosynthetic tissue, making them important photoprotective compounds (Schoenwaelder & Wiencke 2000; Amsler 2008), but also may also an act as antifouling agent or feeding deterrant (Stengel et al. 2011).

Salt stress significantly influences the physiology and biochemistry of seaweeds (Spurkland & Iken 2011). In the face of salt or osmotic stress, brown seaweeds and some groups of red

seaweeds can produce storage compounds such as carbohydrates (mannitol) (Reed et al. 1985; Karsten et al. 1992), to preserve cellular functions during osmotic stress (Eggert et al. 2007). In brown seaweed such as *Ectocarpus siliculosus*, it has been suggested that mannitol acts mainly as a local osmoprotectant or osmolyte against salt stress (Dittami et al. 2011). A positive correlation has been observed between high temperature and low salinity, affecting photosynthetic activity of the species *Laminaria solindungula* (Diehl et al. 2020). Notably, in the presence of low temperatures, a high concentration of mannitol has also been observed in brown algae such as *Saccharina latissima* (Elliot et al. 2017; Monteiro et al. 2021).

In the ecophysiological study of seaweeds, physiological and biochemical parameters such as those mentioned above are generally used as sensitive indicators of the changes produced by stress.

1.6 *Stress - causing factors*

Stress is defined as "the impact of any set of abiotic and biotic factors that negatively affect individual performance, ultimately impairing population growth rate through reduced individual survival, growth or reproduction" (Grime 1989; Vinebrooke et al. 2004). Stress can be induced by a range of both biotic and abiotic factors (Schmitz et al. 1997; Vinebrooke et al. 2004), but whether a factor is considered a stressor will depend on the organism as such, with the duration and recurrence of stress, and interactions between factors (Wahl et al. 2011). Focusing on abiotic stressors, the stress is entirely related to environmental amplitud and how these can exceed tolerance limits (Petchey et al. 1999; McMahon et al. 2012). Abiotic stress in marine environments has been well documented: changes in irradiance levels, *e.g.,* PAR or UV radiation, increased or decreased temperature, decreased pH, osmotic stress, and exposure to toxic chemicals (Davison & Pearson 1996; Schwarzenbach et al. 2006; Bischof et al. 2019). As a result, these environmental changes affect the level of community or ecosystems, generating a disturbance that can be acute or chronic, leading to, *e.g.,* a decrease in the number of organisms (Piliére et al. 2014) or the individual level, where these changes are considered a sublethal effect on an organism's physiology (Nõges et al. 2016). However, species physiology is not fixed; the stress response and tolerance will depend on genetic and phenotypic factors, which vary between individuals (Vinebrooke et al. 2004).

On the other hand, the options that have the organism to respond to environmental change are generally described as "move, adapt or die" (Bischof et al. 2019). However, this phrase excludes the physiological plasticity of species, as environments with a shorter evolutionary history and therefore less stable, such as the Arctic, would tend to exhibit a greater degree of physiological plasticity (Peck et al. 2006; Wiencke and Amsler 2012; Bischof et al. 2019). Finally, stress as such acts as a selective agent directly involving the "tolerance" of the species (Wahl et al. 2011) and how it can respond to biotic-abiotic factors and the intrinsic stress factor itself (Bijlsma & Loeschcke 2005).

1.7 *Desmarestia aculeata* (Linnaeus) J. V. Lamouroux 1813

Desmarestia aculeata (Fig. 5) is a brown seaweed belonging to the order Desmarestiales (Table 1). Due to its morphological structure and functionality, Steneck & Watling (1982) describes it as a branched corticated species. A flattened central axis arises from a basal disc and tapers as it reaches the apical zone. It has flat branches branching alternately and oppositely in the same plane. During spring and summer, small young branches up to 4 mm long emerge (Fernandez 2011). The pigmentation of *D. aculeata* varies with the age of the thallus; while the seaweed is young, it has a greenish pigmentation, and with time the pigmentation changes to brown. *D. aculeata* is a perennial-living species (Mathieson et al. 2000; Hop et al. 2002). *D. aculeata* has a heteromorphic life cycle (Edwards 2000), which a macroscopic phase called sporophytic in which meiosis takes place, and a microscopic filamentous phase or gametophytic (Chapman & Burrows 1970; Nakahara & Nakamura 1971).

Table 1. Taxonomy of brown seaweed *Desmarestia aculeata* (according to Guiry & Guiry, 2022).

Phylum	Ochrophyta
Class	Phaeophyceae
Order	Desmarestiales
Family	Desmarestiaceae
Genus	*Desmarestia*
Species	*Desmarestia aculeata*

This species is widely distributed in the North Atlantic (Mathieson & Dawes 2017; Nielsen & Lundsteen 2019), and the Arctic zone (Wiencke et al. 2004) and is included by Fredriksen et al. (2019) in the list of species described for the Svalbard region. It is mainly found inhabiting the subtidal zone.

It is considered an opportunistic species frequently associated with other species of the same genus or large brown seaweed such as, *e.g., Saccharina latissima* (Kain & Jones 1975; Pehlke & Bartsch 2008), being able to form extensive beds during summer (Conway, 1967). Lippert et al. (2001) describe 36 species of epifaunal organisms living on or around this species, some organisms using it mainly as a refuge, camouflaging themselves in its fronds, *e.g*., amphipods. Finally, studies focusing on the species ecology, ecophysiology, circannual cycles, and reproduction have been conducted in the last 20 years (Conway 1967; Chapman & Burrows 1970; Bischof et al. 2002; Iñiguez et al. 2015; Gordillo et al. 2016).

Fig. 5 Underwater picture of *Alaria esculenta* and *Desmarestia aculeata* sporophyte (yellow arrow), at Brandal point, Kongsfjorden, Arctic. © Sarina Niedzwiedz.

1.8 *Palmaria palmata* (Linnaeus) F. Weber & D. Mohr 1805

Palmaria palmata (Fig. 6) is a red seaweed, belonging to the order Palmariales (Table 2). *P. palmata* is foliose with a frond ranging from 20 to 50 cm in length, which arises from a discoid base (Hill, 2008). Its membranous fronds are characteristically palmate, with a dichotomous termination (Kuipers 2021). The pigmentation of *P. palmata* is dark red when is

adult. With respect to its life cycle, *P. palmata* is characterised by being diplohaplontic. The tetrasporophytic and gametophytic male fronds are macroscopic and the gametophytic female microscopic, characterised by the absence of the carposporophytic phase (Van der Meer & Todd 1980; Le Gall et al. 2004).

Table 2. Taxonomy of red seaweed *Palmaria palmata* (according to Guiry & Guiry, 2022).

Phylum	Rhodophyta
Class	Florideophyceae
Order	Palmariales
Family	Palmariaceae
Genus	*Palmaria*
Species	*Palmaria palmata*

The species *P. palmata* is characterised by a wide distribution in the North Atlantic, including the Arctic zone (Morgan et al. 1980; Mouritsen et al. 2013). It can be found inhabiting the intertidal zone down to 20 m depth (Kuipers 2021). Due to its wide distribution it is commonly found in protected or exposed areas (Irvine & Guiry, 1983), on rocky substrate or on mussels, epiphytic on other seaweeds, and in low salinity areas (Schmedes & Nielsen 2020; Kuipers 2021). Mouritsen et al. (2013) describe how *P. palmata* has been collected for centuries, being considered one of the best known species due to its economic value (Rudolph, 2000). This species has begun to be cultivated in recent years, due to its high use in the aquaculture, food, cosmetics and other industries (Parjikolaei et al. 2013). Due to its importance, *P. palmata* has been extensively studied. Studies based on its ecophysiology, life cycle, ecology, nutritional value and chemical compounds, to name a few, have been crucial to understanding the biology of this species (Hanelt & Nultsch 1995; Aguilera et al. 2002; Gordillo et al. 2006).

Fig. 6 Picture of the red seaweed *Palmaria palmata*, a species collected in the intertidal zone off the coast of Ny Ålesund, Kongsfjorden, Arctic. © Johanna Marambio.

2. Aim, Research Questions and Hypothesis

2.1 *Aim and Research questions*

Several environmental factors affect the ecophysiology of benthic seaweeds in the Arctic, and these environmental factors are modulated by the current process of global climate warming. The aim of this study is to delve into the ecophysiological acclimation processes of two species of seaweeds present in the Arctic: *Desmarestia aculeata* and *Palmaria palmata*, both of temperate-Arctic distribution. The study focuses on the short-term ecophysiological and biochemical response of both species to variations in environmental factors such as temperature, irradiance and salinity. This study provides important information on the current and future response of Arctic seaweed species to the increasing impact of climate change in polar marine environments.

In particular, this study aims to answer the following questions:

1. What is the effect of the interaction between temperature and irradiance on the photosynthetic and internal biochemical regulation of the species *D aculeata* and *P. palmata*?

2. How does hyposalinity affect the regulation of photosynthetic and biochemical processes in *P. palmata* during daily light cycles?

3. Are adult sporophytes of *D. aculeata* able to regulate their internal photosynthetic and biochemical processes during alternating high and low irradiance under hyposalinity conditions?

2.2 *Thesis outline and hypotheses*

The ecophysiology of algae of ecological and economic interest can be affected by climate change and its related drivers such as temperature, irradiance, and salinity (Hanelt & Nultsch 1995; Hanelt et al. 1997; Karsten et al. 2003; Wiencke et al. 2007; Wiencke & Amsler 2012). Currently, many of the research papers covering these issues in seaweeds are based on mono-factorial studies and not on the interaction of factors (Bischof et al. 2006; Bartsch et al. 2008; Simonson et al. 2015; but see: *e.g.*, Karsten et al. 2003; Fredersdorf et al. 2009; Zacher et al.

2016; Martins et al. 2017; Diehl et al. 2020; Monteiro et al. 2021). After exposing the algae to interaction between drivers, seaweed exhibit a series of photosynthetic and biochemical responses, with which they can regulate its internal metabolism. This acclimation will depend on the intensity of the drivers and the duration of exposure to these conditions (Hurd et al. 2014). Consequently, the present study focuses on the interaction of short-term factors in two species inhabiting the Arctic zone, *D. aculeata* (brown seaweed) and *P. palmata* (red seaweed). The interaction between temperature - irradiance and salinity - irradiance (daily irradiance cycles) was studied in both species.

Publication I

Climate change is driving changes in the temperature regime and increasing ice-free zones, resulting in higher irradiance levels in the water column in Arctic fjord systems, directly affecting the algal species that inhabit them. **Publication I** describes the acclimation potential of two seaweeds species *D. aculeata* (Phaeophyceae) and *P. palmata* (Rhodophyta), which inhabit Kongsfjorden, Arctic, and are characterised by a similar temperate-Arctic distribution. Both species were exposed in the laboratory to the interaction of environmental factors such as temperature and different irradiance levels that simulate Arctic summer conditions. This experiment was carried out to evaluate the response of photosynthetic and biochemical parameters of both species.

Hypothesis I: The similar geographical distribution of *D. aculeata* and *P. palmata* will be reflected in similar ecophysiological acclimation mechanisms, under the interaction of drivers such as temperature and irradiance.

Publication II

The increase in temperature has generated a series of changes in Arctic fjords. In particular, the melting of glaciers typically results in an increase in the discharge of low salinity water into Arctic fjord systems. In addition, seaweeds are also affected by high irradiance in the water column under summer conditions and the diminishing influence of sea ice. For this reason, **publication II** directly addresses the effect of daily irradiance cycles during the Arctic summer on *P. palmata*, and how the regulation of photosynthetic and biochemical processes is affected by hyposalinity conditions. This study was carried out to understand its short-term acclimation capacity.

Hypothesis II: Hyposalinity will affect photosynthetic and biochemical regulation of the interdital seaweed *P. palmata*, during daily light cycles simulating the Arctic summer.

Publication III

Large brown algal meadows are frequently present in Arctic fjords, one of the main species being the brown alga *D. aculeata*. The increase in meltwater, due to temperature increases caused by climate change, directly affects coastal seaweed populations. The species *D. aculeata*, tends to be subtidal, however, populations in the lower intertidal can also be observed on the Arctic coast. In this context, for **publication III**, specimens of *D. aculeata*, which inhabits the lower intertidal coastal zone of Ny Ålesund, Kongsfjorden, were collected. These specimens were subjected to low salinity and alternate irradiance (high and low) conditions. This study was carried out to evaluate their ability to acclimation to different levels of short-term irradiance and how this is affected by hyposalinity.

Hypothesis III: Hyposalinity will affect the process of ecophysiological acclimation to high and low irradiance of the Arctic fjord species *D. aculeata*, reflected in the photosynthetic activity and biochemical content.

3. List of Publications and Declaration of Contributions

Publication I:

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

Authors: **J. Marambio** & K. Bischof

Journal: *Polar Research* (2021), 40: 5702

http://dx.doi.org/10.33265/polar.v40.5702

Contribution of the candidate in % of the total workload

Experimental concept and design: 90 %

Experimental work and acquisition of the data: 95 %

Data Analysis and interpretation: 90 %

Preparation of figures and tables: 100 %

Drafting of the manuscript: 95 %

Publication II:

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

Authors: **J. Marambio**, S. Rosenfeld & K. Bischof

Journal: *Journal of Photochemistry and Photobiology* (2022), 11: 100124

https://doi.org/10.1016/j.jpap.2022.100124

Contribution of the candidate in % of the total workload

Experimental concept and design: 95 %

Experimental work and acquisition of the data: 100 %

Data Analysis and interpretation: 80 %

Preparation of figures and tables: 100 %

Drafting of the manuscript: 95%

Publication III:

Title: High ecophysiological plasticity of *Desmarestia aculeata* (Phaeophyceae) from an Arctic fjord under varying salinity and irradiance conditions

Authors: **J. Marambio**, N. Diehl & K. Bischof

Journal: Submitted to *Biology*, special issue "Polar Ecosystem: Response of Organisms to Changing Climate"

Contribution of the candidate in % of the total workload

Experimental concept and design: 95 %

Experimental work and acquisition of the data: 100 %

Data Analysis and interpretation: 80 %

Preparation of figures and tables: 90 %

Drafting of the manuscript: 95 %

Date: 01 September 2022

Signature:

4. Publication I

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

J. Marambio & K. Bischof

Desmarestia aculeata & Palmaria palmata

RESEARCH ARTICLE

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

Keywords
Arctic; *Desmarestia aculeata*; *Palmaria palmata*; photosynthesis; temperature; irradiance

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Abbreviations
α: photosynthetic efficiency
ANOVA: analysis of variance
Anthera: antheraxanthin
Apc: allophycocyanin
β-car: β-carotene
chl *a*: chlorophyll *a*
chl *c2*: chlorophyll *c2*
DPPH: 2,2-diphenyl-1-picrylhydrazyl
DPS: de-epoxidation state
DW: dry weight
Ek: saturation irradiance
Fuco: fucoxanthin
F_v/F_m: maximal quantum yield of PSII
Lut: lutein
PAR: photosynthetically active radiation
Pc: phycocyanin
Pe: phycoerythrin
PSII: photosystem II
P-E: photosynthesis–irradiance
rETRmax: maximum relative electron transport rate
ROS: reactive oxygen species
SD: standard deviation
TE: Trolox equivalent
Trolox: 6-hydroxy-2,5,7,8-tetramethylchroman-2carboxylic acid
Tukey's HSD: Tukey's honestly significant difference test
UV: ultraviolet
VAZ: violaxanthin, antheraxanthin, zeaxanthin
Viol: violaxanthin
Zeax: zeaxanthin

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

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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

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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 $\lambda = 730$ 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

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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

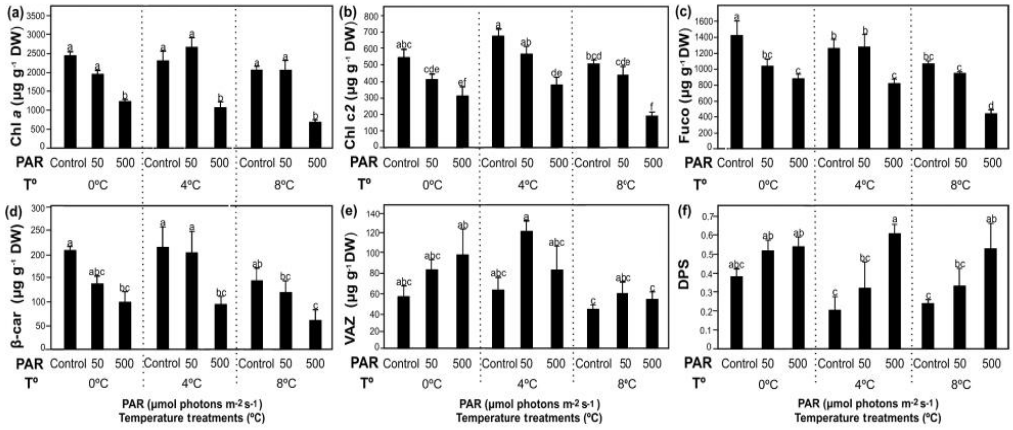

Fig. 1 Mean±SD pigment concentrations (n=3) in *Desmarestia aculeata*. For the pigments chl *a*, chl *c2*, Fuco, β-car, the table shows the pool size of the xanthophylls (VAZ) and de-epoxidation status of the xanthophyll cycle (DPS) in (µg g $^{-1}$ DW). Samples at three different temperatures (0, 4 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,

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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

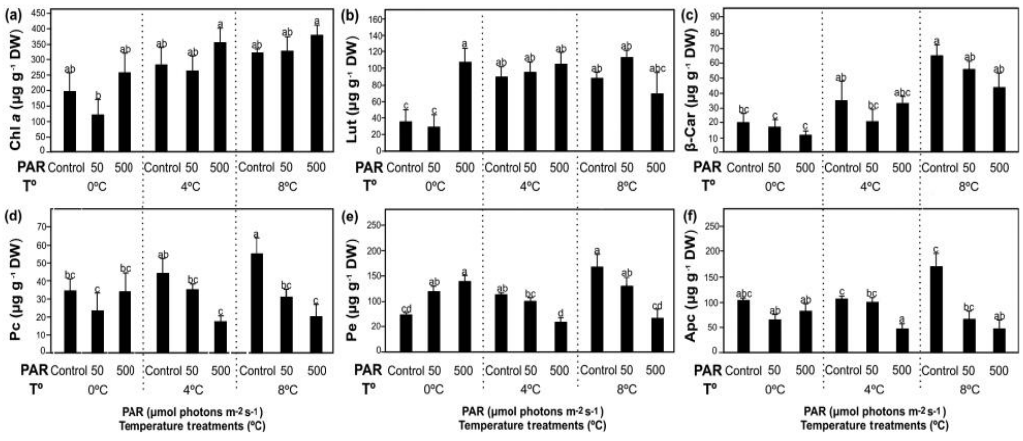

Fig. 2 Mean±SD pigment concentration ($n=3$) in *Palmaria palmata*. For pigments chl *a*, Lut, β-car, Pc, Pe and Apc in (µg g^{-1} DW). Samples at three different temperatures (0, 4 and 8°C) and different light intensities: Control (Initial control measure 50 µmol photons m^{-2} s^{-1}), 50 and 500 µmol 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).

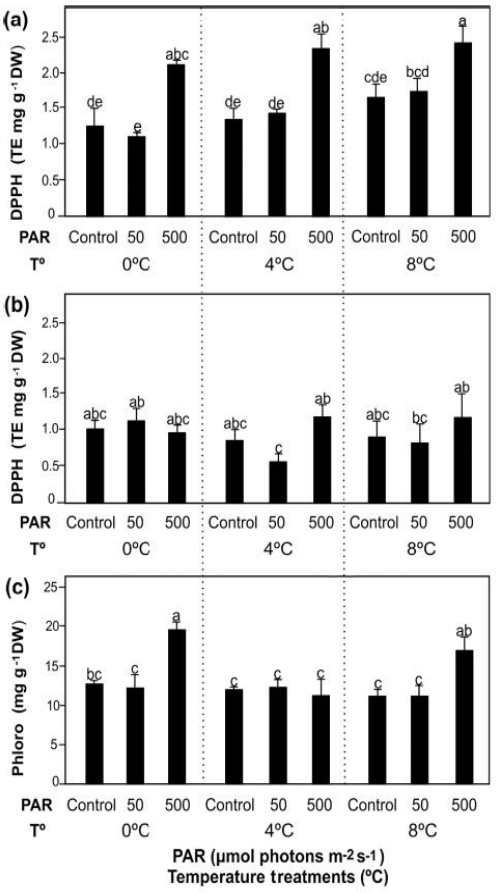

Fig. 3 Antioxidant activity (n=3) is shown for (a) *Desmarestia aculeata* DPPH (TE mg g^{-1} DW) (b) *Palmaria palmata* DPPH (TE mg g^{-1} DW), and (c) *D. aculeata* phlorotannins (mg g^{-1} DW). Samples at three different temperatures (0, 4 and 8°C) and different light intensities: control (initial 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 ($p < 0.05$).

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).

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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

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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 photoprotective 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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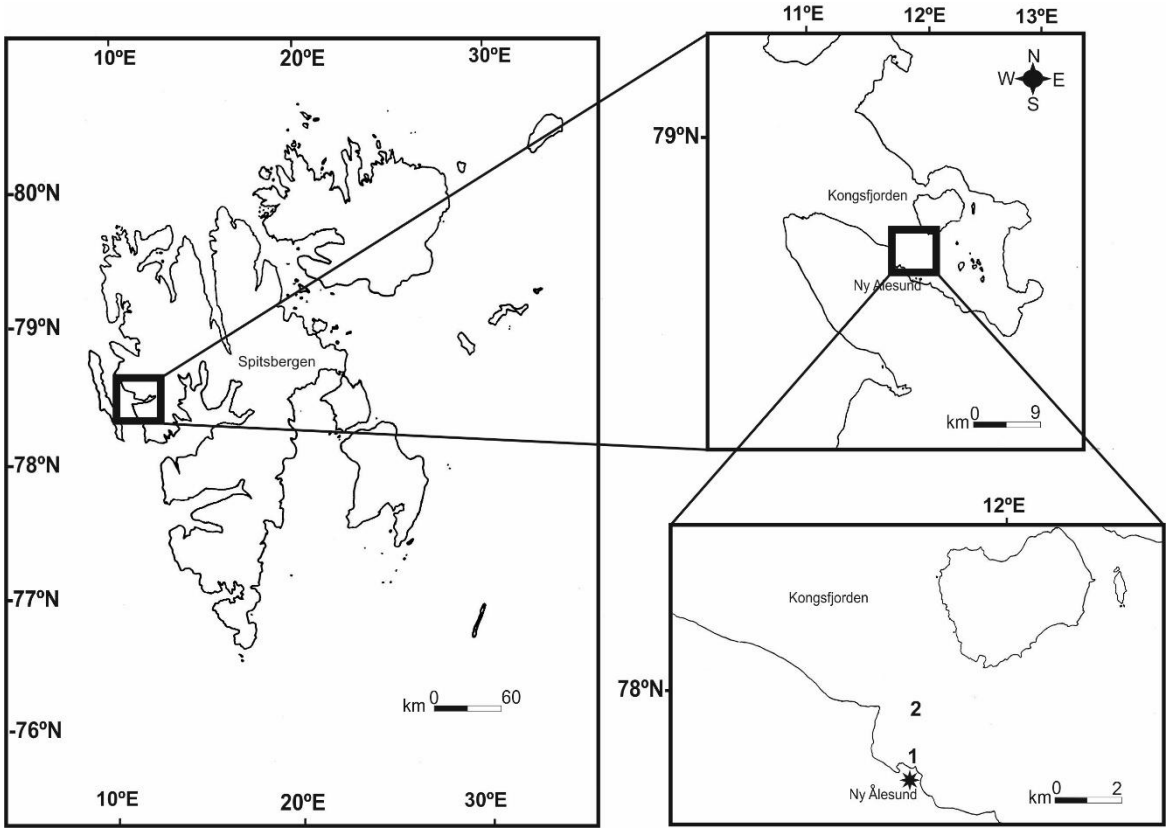

Supplementary Fig. 1 Map of Kongsfjorden, Spitsbergen, Svalbard (78.9° N, 11.9° E). The specimens were collected at two sites: (1) *Palmaria palmata* was collected in front of the Ny-Ålesund Marine Laboratory (78°55'39.8"N; 11°55'48.3"E) and (2) *Desmarestia aculeata* was collected at Brandal (78º56'49.25"N; 11º51'25.03"E).

Supplementary Table 1. Results of two-way ANOVA, Tukey's HSD for effects of temperature and light on algal photosynthetic parameters in *D. aculeata* and *P. palmata*. Statistically significant values are in boldface ($p < 0.05$).

Species	Variable	Factor	*df*	*p* value
D. aculeata	F_v/F_m	Temperature	2	0.0680
		Light	2	<0.0001
		Temperature × light	4	0.3455
	rETRmax	Temperature	2	0.0946
		Light	2	0.0031
		Temperature × light	4	0.3590
	α	Temperature	2	0.2910
		Light	2	<0.0001
		Temperature × light	4	0.1437
	*E*k	Temperature	2	0.1455
		Light	2	0.0003
		Temperature × light	4	0.2596
P. palmata				
	F_v/F_m	Temperature	2	<0.0001
		Light	2	0.0005
		Temperature × light	4	0.0006
	rETRmax	Temperature	2	0.0471
		Light	2	0.0054
		Temperature × light	4	0.1911
	α	Temperature	2	0.1772
		Light	2	0.0167
		Temperature × light	4	0.1492
	*E*k	Temperature	2	<0.0001
		Light	2	0.0527
		Temperature × light	4	0.1961

Supplementary Table 2. Results of two-way ANOVA, Tukey's HSD for effects of temperature and light on algal pigments and antioxidant activity in *Desmarestia aculeata* and *Palmaria palmata*. Statistically significant values are in boldface ($p < 0.05$).

Species	Variable	Factor	*df*	*p* value
D. aculeata				
	chl *a*	Temperature	2	0.0781
		Light	2	<0.0001
		Temperature × light	4	0.2450
	chl *c2*	Temperature	2	0.1655
		Light	2	<0.0001
		Temperature × light	4	0.0904
	Fuco	Temperature	2	<0.0001
		Light	2	<0.0001
		Temperature × light	4	<0.0001
	β-car	Temperature	2	0.0007
		Light	2	<0.0001
		Temperature × light	4	0.2123
	Viol	Temperature	2	<0.0001
		Light	2	<0.0001
		Temperature × light	4	<0.0001
	Anthera	Temperature	2	<0.0053
		Light	2	0.0246
		Temperature × light	4	0.3840
	Zeax	Temperature	2	0.7418
		Light	2	<0.0001
		Temperature × light	4	0.6097
	VAZ	Temperature	2	0.0044
		Light	2	0.4384
		Temperature × light	4	0.2865
	Fuco:chl *a*	Temperature	2	0.0713
		Light	2	0.0047
		Temperature × light	4	0.1533
	β-car:chl *a*	Temperature	2	0.0661
		Light	2	0.3967
		Temperature × light	4	0.4102
	Zeax:chl *a*	Temperature	2	0.5419
		Light	2	<0.0001
		Temperature × light	4	0.3808
	Anthera:chl *a*	Temperature	2	0.0310
		Light	2	0.0145

Species	Variable	Factor	*df*	*p* value
		Temperature × light	4	0.8082
	Viol:chl *a*	Temperature	2	<0.0001
		Light	2	0.0028
		Temperature × light	4	<0.0001
	chl *c2*:chl *a*	Temperature	2	<0.0001
		Light	2	0.1021
		Temperature × light	4	0.7901
	DPS	Temperature	2	0.0290
		Light	2	<0.0001
		Temperature × light	4	0.1030
	(chl *c2*+Fuco)/chl *a*	Temperature	2	0.8315
		Light	2	0.6941
		Temperature × light	4	0.0654
	VAZ:chl *a*	Temperature	2	0.0840
		Light	2	0.3574
		Temperature × light	4	0.1522
	DPPH	Temperature	2	0.0012
		Light	2	<0.0001
		Temperature × light	4	0.6240
	Phlorotannins	Temperature	2	0.0939
		Light	2	0.0151
		Temperature × light	4	0.2857
P. palmata				
	chl *a*	Temperature	2	0.1851
		Light	2	0.0889
		Temperature × light	4	0.6641
	Lut	Temperature	2	0.0328
		Light	2	0.0016
		Temperature × light	4	0.1863
	β-car	Temperature	2	0.0015
		Light	2	0.6439
		Temperature × light	4	0.0548
	Pc	Temperature	2	0.2264
		Light	2	<.0001
		Temperature × light	4	0.0831
	Pe	Temperature	2	0.0019
		Light	2	<0.0001
		Temperature × light	4	<0.0001
	Apc	Temperature	2	0.0122
		Light	2	0.0014
		Temperature × light	4	0.0191

Species	Variable	Factor	*df*	*p* value
	(Apc+Pc+Pe)/chl *a*	Temperature	2	0.0066
		Light	2	0.0193
		Temperature × light	4	<0.0001
	Pc:chl *a*	Temperature	2	0.1941
		Light	2	0.0002
		Temperature × light	4	<0.0001
	Pe:chl *a*	Temperature	2	0.2592
		Light	2	0.0341
		Temperature × light	4	0.3540
	Apc:chl *a*	Temperature	2	0.0010
		Light	2	0.0345
		Temperature × light	4	<0.0001
	DPPH	Temperature	2	0.4314
		Light	2	0.0266
		Temperature × light	4	0.1767

Supplementary Table 3. Mean±SD pigment concentration (µg g^{-1} DW) (n = 3) in *Desmarestia aculeata.* Light intensities were: 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	Viol (µg g^{-1} DW)	Anthera (µg g^{-1} DW)	Zeax (µg g^{-1} DW)
0	Control	25.00 (±7.83)^{a}	24.33 (±9.02)^{a}	17.66 (±5.50)^{b}
	50	13.00 (±1.73)^{b}	12.46 (±5.28)^{bc}	39.01 (±19.15)^{ab}
	500	17.44 (±6.11)^{ab}	10.67 (±2.85)^{bc}	82.33 (±7.57)^{a}
4	Control	60.33 (±8.02)^{c}	8.33 (±5.85)^{bc}	19.06 (±12.50)^{b}
	50	59.01 (±8.18)^{c}	5.07 (±1.05)^{bc}	21.66 (±9.35)^{ab}
	500	21.67 (±5.74)^{ab}	7.33 (±2.09)^{bc}	116.31 (±22.18)^{a}
8	Control	39.01 (±8.00)^{bc}	6.31 (±1.13)^{bc}	16.05 (±2.51)^{b}
	50	20.33 (±8.38)^{a}	3.44 (±0.95)^{bc}	15.00 (±3.11)^{b}
	500	10.80 (±2.58)^{d}	3.13 (±0.55)^{c}	95.26 (±15.85)^{a}

Supplementary Table 4. Pigment ratios ($n = 3$) for *Desmarestia aculeata.* Light intensities were: 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)	Treat-ment	Fuco:chl *a*	β-car:chl *a*	Zeax:chl *a*	Anthera:chl *a*	Viol:chl *a*	chl *c2*:chl *a*	(chl *c2* +Fuco)/ chl *a*	VAZ:chl *a*
0	Control	0.997(±0.06)^{a}	0.085(±0.01)^{a}	0.007(±0.01)^{b}	0.010(±0.004)^{ac}	0.062(±0.001)^{a}	0.224(±0.01)^{bc}	0.748(±0.09)^{ab}	0.033(±0.01)^{ab}
	50	0.535(±0.07)^{bc}	0.071(±0.01)^{ab}	0.020(±0.01)^{b}	0.006(±0.001)^{bcd}	0.007(±0.001)^{e}	0.211(±0.02)^{c}	0.762(±0.02)^{ab}	0.069(±0.02)^{ab}
	500	0.721(±0.02)^{bc}	0.080(±0.02)^{a}	0.067(±0.01)^{ab}	0.013(±0.002)^{a}	0.023(±0.006)^{bc}	0.250(±0.03)^{bc}	0.612(±0.03)^{ab}	0.037(±0.01)^{ab}
4	Control	0.560(±0.11)^{bc}	0.093(±0.01)^{a}	0.009(±0.01)^{b}	0.004(±0.003)^{bcd}	0.026(±0.004)^{b}	0.298(±0.04)^{abc}	0.672(±0.05)^{ab}	0.054(±0.01)^{ab}
	50	0.626(±0.06)^{bc}	0.098(±0.02)^{a}	0.011(±0.01)^{b}	0.003(±0.003)^{d}	0.029(±0.001)^{b}	0.312(±0.01)^{ab}	1.140(±0.24)^{a}	0.138(±0.01)^{a}
	500	0.782(±0.18)^{ab}	0.091(±0.03)^{a}	0.108(±0.03)^{ab}	0.009(±0.002)^{abc}	0.021(±0.008)^{bcd}	0.358(±0.05)^{ab}	0.805(±0.04)^{ab}	0.091(±0.06)^{ab}
8	Control	0.523(±0.03)^{c}	0.070(±0.01)^{ab}	0.008(±0.01)^{b}	0.003(±0.001)^{cd}	0.019(±0.004)^{bcd}	0.248(±0.02)^{bc}	0.911(±0.12)^{ab}	0.089(±0.09)^{ab}
	50	0.468(±0.07)^{c}	0.057(±0.01)^{b}	0.007(±0.01)^{b}	0.002(±0.001)^{d}	0.010(±0.004)^{de}	0.212(±0.01)^{c}	1.105(±0.25)^{b}	0.026(±0.01)^{b}
	500	0.634(±0.08)^{bc}	0.091(±0.04)^{a}	0.141(±0.11)^{a}	0.007(±0.001)^{bcd}	0.013(±0.002)^{cde}	0.277(±0.03)^{abc}	0.759(±0.03)^{b}	0.029(±0.01)^{b}

Supplementary Table 5. Pigment ratios ($n = 3$) for *Palmaria palmata.* The different light intensities were: 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	(Apc+Pc+Pe)/chl *a*	Pc:chl *a*	Pe:chl *a*	Apc:chl *a*
0	Control	0.204(±0.02)^{d}	0.331(±0.03)^{c}	0.071(±0.01)^{a}	0.099(±0.02)^{bc}
	50	0.220(±0.02)^{cd}	0.258(±0.11)^{c}	0.130(±0.03)^{b}	0.069(±0.03)^{c}
	500	0.647(±0.07)^{a}	0.869(±1.52)^{b}	0.162(±0.04)^{b}	0.203(±0.04)^{a}
4	Control	0.382(±0.01)^{bc}	0.664(±0.19)^{bc}	0.166(±0.02)^{b}	0.156(±0.02)^{ab}
	50	0.392(±0.03)^{bc}	0.596(±0.20)^{bc}	0.169(±0.07)^{b}	0.166(±0.01)^{ab}
	500	0.291(±0.01)^{bcd}	0.432(±0.06)^{bc}	0.140(±0.02)^{b}	0.110(±0.01)^{b}
8	Control	0.371(±0.02)^{b}	0.035(±0.09)^{c}	0.132(±0.04)^{b}	0.146(±0.03)^{ab}
	50	0.213(±0.01)^{cd}	0.029(±0.07)^{c}	0.123(±0.04)^{b}	0.063(±0.02)^{c}
	500	0.168(±0.01)^{d}	0.025(±0.07)^{a}	0.084(±0.01)^{a}	0.057(±0.01)^{c}

5. Publication II

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

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Palmaria palmata

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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 occurence 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

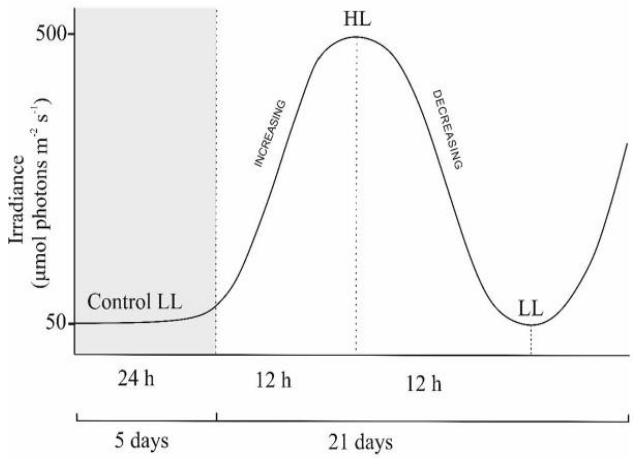

Fig. 1. Experimental low light/high light cycle for exposure of specimens of *Palmaria palmata* at three salinities. (a) The grey band shows the "Pre-control treatment" period (5 days) at 50 µmol photons m^{-2} s^{-1}. Subsequently, the daily light cycle is shown, with the lowest irradiance (LL) at 50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

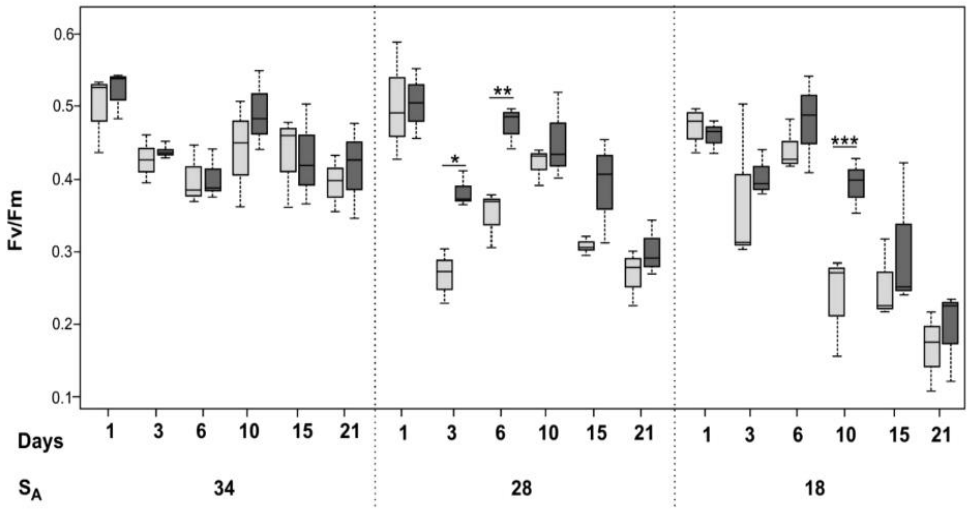

Fig. 2. Mean±SD for F_v/F_m ($n = 3$) in *Palmaria palmata*. Samples at three different salinities (S_A 34, 28, and 18) and two different light points: LL at 50 µmol photons m^{-2} s^{-1} (dark grey) and HL at 500 µmol photons m^{-2} s^{-1} (light grey). Measurements are represented from days 1 to 21.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

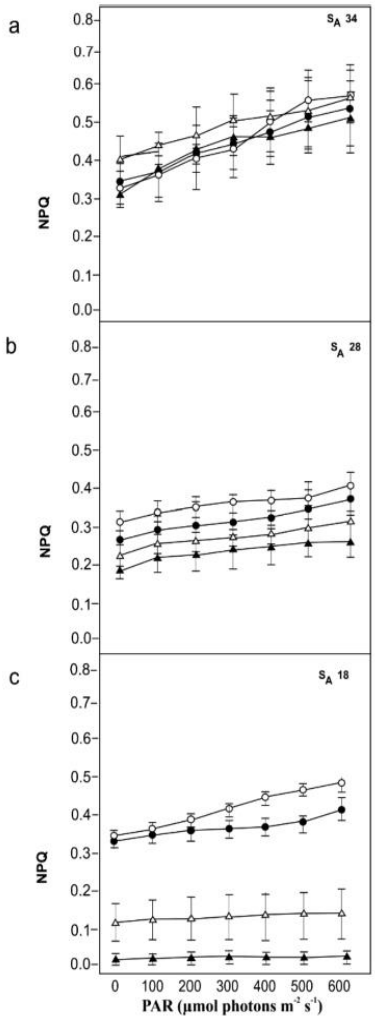

Fig. 3. Mean±SD of NPQ ($n = 3$) for *Palmaria palmata*. Measurements plotted for days 1 (circles) and 21 (triangle). Two light points are LL at 50 µmol photons m^{-2} s^{-1} (black) and HL at 500 µmol photons m^{-2} s^{-1} (white). Measurements were performed at the three salinities analysed (S_A 34,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

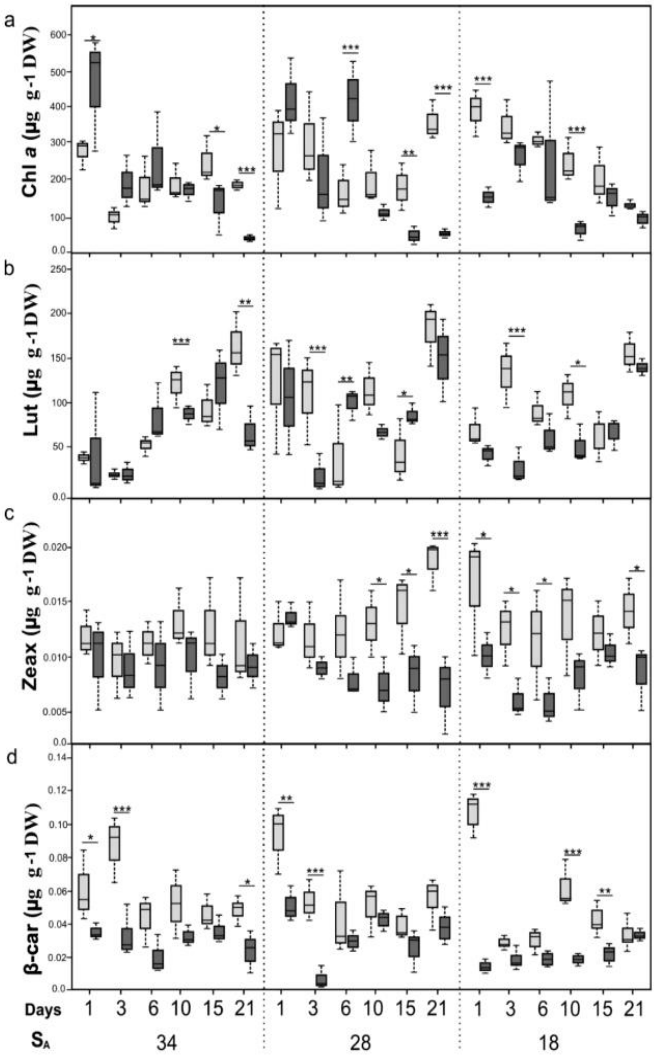

Fig. 4. Mean±SD pigment concentration (n = 3) in *Palmaria palmata*. For pigments, Chlorophyll *a* (Chl *a*), Lutein (Lut), Zeaxanthin (Zeax), and β-Carotene (β-Car) in (µg g^{-1} DW). Samples at three different salinities (S_A 34, 28, and 18) and two different light points LL at 50 µmol photons m^{-2} 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).

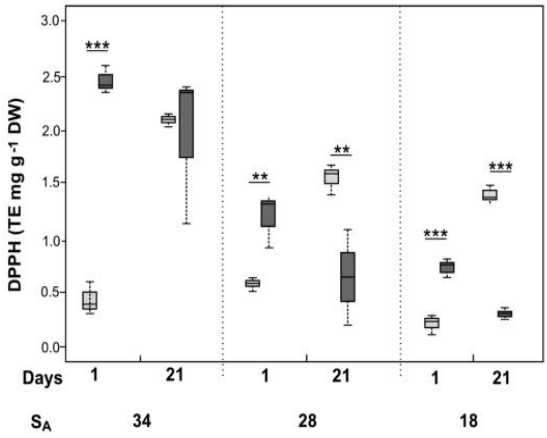

Fig. 5. Antioxidant activity DPPH Mean±SD (n = 3) in *Palmaria palmata*. Samples at three different salinities (S_A 34, 28, and 18) and two different light intensities LL at 50 µmol photons m^{-2} s^{-1} (dark grey) and HL at 500 µmol photons m^{-2} s^{-1} (light grey). Measurements represented for days 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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Supplementary Material 1. Results of three-way ANOVA for *Palmaria palmata*: effects of light points, salinity, and time for F_v/F_m and HPLC pigment concentration Chl *a*, Lut, Zeax. An asterisk indicates statistically significant values: (***) p<0.0001, (**) p<0.001, (*) p<0.01.

	Variable	Factor	*df*	*p*-value	
Photosynthetic parameter	F_v/F_m	Time	5	<0.001	***
		Light	1	<0.001	***
		Salinity	2	<0.001	***
		Time: Light	5	0.403	
		Time:Salinity	10	<0.001	***
		Light:Salinity	2	0.170	
		Time:Light:Salinity	10	0.411	
Pigments					
	Chl *a*	Time	5	<0.001	***
		Light	1	<0.001	***
		Salinity	2	0.750	
		Time: Light	5	<0.001	***
		Time:Salinity	10	<0.001	***
		Light:Salinity	2	0.012	*
		Time:Light:Salinity	10	<0.001	***
	Lut	Time	5	<0.001	***
		Light	1	0.003	**
		Salinity	2	0.035	*
		Time: Light	5	<0.001	***
		Time:Salinity	10	<0.001	***
		Light:Salinity	2	0.123	
		Time:Light:Salinity	10	0.030	*
	Zeax	Time	5	0.102	
		Light	1	<0.001	***
		Salinity	2	0.034	*
		Time: Light	5	0.540	
		Time:Salinity	10	0.903	
		Light:Salinity	2	0.232	
		Time:Light:Salinity	10	0.341	

Supplementary Material 2. Results of GLM for *Palmaria palmata*: effects of time, salinity, PAR (photosynthetically active radiation) and light points for NPQ and effects of time, salinity and light points for β-Car, Lut: Chl *a*, Zeax: Chl *a*, β-Car: Chl *a* and DPPH. An asterisk indicates statistically significant differences: (***) p<0.0001, (**) p<0.001, (*) p<0.01.

	Variable	Factor	Df	Deviance Resid.	Df	Resid. Dev	Pr (>Chi)	
Photosynthetic parameter	NPQ	Time	1	8.322	250	96.687	<2.2e-16	***
		Salinity	2	20.099	248	76.588	<2.2e-16	***
		PAR	6	3.686	242	72.902	2.112e-13	***
		Light	1	0.700	241	72.203	<0.000	***
		Time: Salinity	2	40.321	239	31.882	<2.2e-16	***
		Time: PAR	6	0.038	233	31.844	0.993	
		Salinity: PAR	12	0.087	221	31.757	0.999	
		Time: Light	1	0.072	220	31.685	0.238	
		Salinity:Light	2	1.408	218	30.278	1.196e-06	***
		PAR:Light	6	0.011	212	30.267	0.999	
		Time: Salinity: PAR	12	0.244	200	30.023	0.966	
		Time: Salinity: Light	2	21.623	198	8.399	<2.2e-16	***
		Time: PAR: Light	6	0.051	192	8.348	0.985	
		Salinity: PAR: Light	12	0.027	180	8.321	0.999	
		Time: Salinity: PAR: Light	12	0.110	168	8.211	0.999	
Pigments	β-Car	Time	5	4.529	102	35.981	<1.506e-06	***
		Light	1	11.722	101	24.259	<2.2e-16	***
		Salinity	2	0.888	99	23.371	0.032	*
		Time: Light	5	1.692	94	21.679	0.022	*
		Time:Salinity	10	3.224	84	18.455	0.005	**
		Light:Salinity	2	1.310	82	17.144	0.006	**
		Time:Light:Salinity	10	6.942	72	10.202	5.65e-08	***

Lut:Chl *a*	Time	5	39.757	103	42.031	<2.2e-16	***
	Light	1	6.399	101	35.632	6.658e-10	***
	Salinity	2	0.884	99	34.748	0.071	
	Time: Light	5	7.763	94	26.985	8.094e-09	***
	Time:Salinity	10	7.144	84	19.841	5.966e-06	***
	Light:Salinity	2	0.930	82	18.911	0.062	
	Time:Light:Salinity	10	4.852	72	14.059	0.001	**
Zeax:Chl *a*	Time	5	16.483	102	36.349	1.6e-15	***
	Light	1	2.089	101	34.260	0.002	**
	Salinity	2	0.750	99	33.510	0.1667	
	Time: Light	5	5.092	94	28.418	<0.000	***
	Time:Salinity	10	7.083	84	21.335	<0.000	***
	Light:Salinity	2	0.068	82	31.267	0.850	
	Time:Light:Salinity	10	4.788	72	16.479	0.011	*
β-Car:Chl *a*	Time	5	12.460	102	57.017	5.407e-12	***
	Light	1	0.053	101	56.964	0.609	
	Salinity	2	3.700	99	53.264	<0.000	***
	Time: Light	5	19.956	94	33.307	<2.2e-16	***
	Time:Salinity	10	10.062	84	23.246	2.873e-07	***
	Light:Salinity	2	0.337	82	22.909	0.434	
	Time:Light:Salinity	10	7.448	72	15.459	5.908e-05	***

Antioxidant activity								
	DPPH	Time	5	12.969	102	28.376	<2.2e-16	***
		Light	1	0.547	101	37.828	0.016	*
		Salinity	2	2.477	99	25.352	2.142e-06	***
		Time: Light	5	9.235	94	16.117	<2.2e-16	***
		Time:Salinity	10	4.402	84	11.715	1.213e-06	***
		Light:Salinity	2	0.310	82	11.405	0.195	
		Time:Light:Salinity	10	3.405	72	8.000	8.764e-05	***

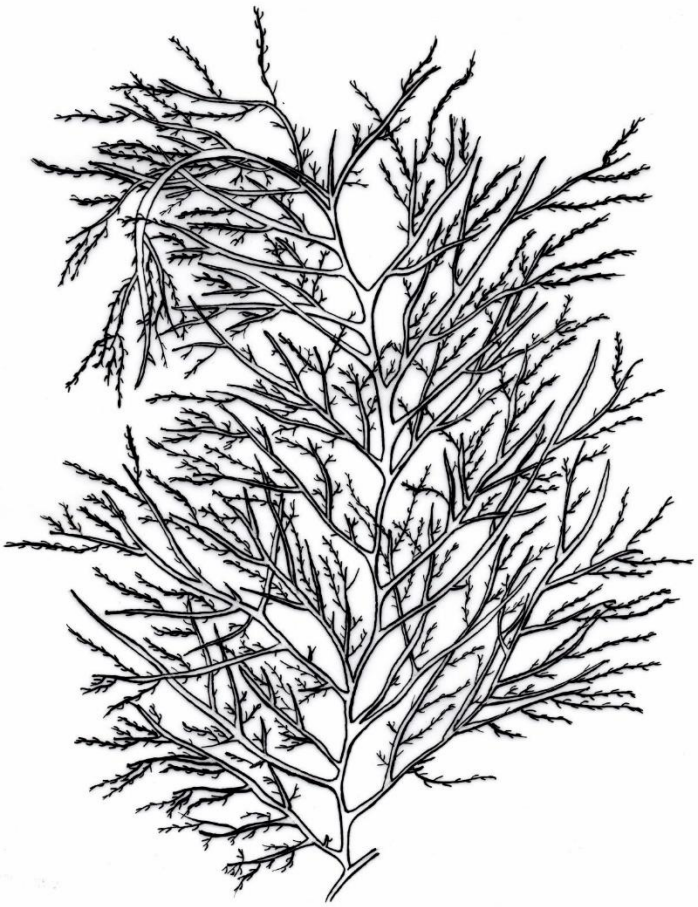
Supplementary Material 3. Results of two-way ANOVA for *Palmaria palmata*: effects of light points and salinity for pigment concentration Allophycocyanin (APC), Phycoerythrin (PE), and Phycocyanin (PC). Statistically significant values are indicated by asterisk: (***) p<0.0001, (**) p<0.001, (*) p<0.01.

	Variable	Factor	*df*	*p*-value	
Pigments	APC	Light	3	<0.001	***
		Salinity	2	0.333	
		Light: Salinity	6	0.087	
	PE	Light	3	<0.001	***
		Salinity	2	0.001	**
		Light: Salinity	6	<0.001	***
	PC	Light	3	<0.001	***
		Salinity	2	0.159	
		Light: Salinity	6	0.090	

6. Publication III

High ecophysiological plasticity of *Desmarestia aculeata* (Phaeophyceae) from an Arctic fjord under varying salinity and irradiance conditions

J. Marambio, N. Diehl & K. Bischof



Desmarestia aculeata

biology

MDPI

Article

High Ecophysiological Plasticity of *Desmarestia aculeata* (Phaeophyceae) Present in an Arctic Fjord under Varying Salinity and Irradiance Conditions

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Simple Summary: The Arctic region has been affected by rising temperatures, directly affecting the organisms living there. One of the organisms that inhabit this area is the seaweed *Desmarestia aculeata* (Phaeophyceae), widely distributed in the North Atlantic. It is exposed to the high Arctic light regime and fluctuating salinity conditions from glacial and terrestrial run-off. Despite its abundance, little is known about *D. aculeata* and how environmental drivers will affect it in a future altered by climate change. During the summer of 2019, *D. aculeata* was collected in Kongsfjorden, Svalbard (78.9° N, 11.9° E) to investigate its physiological and biochemical responses to salinities of 34, 28, and 18, and daily cycles of irradiance (50–500 µmol photons $m^{-2}s^{-1}$) at 0 °C over 21 days. Photosynthetic parameters and high pigment concentrations show how this species has an effective acclimation to irradiance changes, being unaffected by low salinity. The high concentration of antioxidant phlorotannins at low salinity show how *D. aculeata* can regulate its daily cycle despite the hyposaline conditions. Salinity and light are interacting factors in the acclimation process. Our work shows the high plasticity of *D. aculeata*, such that the species will probably be able to tolerate future changes in the Arctic.

Abstract: The seaweed *Desmarestia aculeata* (Phaeophyceae) is distributed in the temperate zone of the North Atlantic up to the Arctic, where it is exposed to a high Arctic light regime and fluctuating salinity conditions resulting from glacial and terrestrial run-off. Information on how this species is able to thrive under current and future Arctic conditions is scarce. During the Arctic summer of 2019, *D. aculeata* was collected in Kongsfjorden, Svalbard (78.9° N, 11.9° E) to investigate its physiological and biochemical responses to variations in salinity (salinities: 34, 28 and 18) and daily cycles of irradiance (50–500 µmol photons $m^{-2}s^{-1}$) at 0 °C over 21 days. The species revealed effective short-term acclimation to both abiotic drivers. Maximal quantum yield of PSII (F_v/F_m) fluctuated with the light cycle at a salinity of 34, while the maximum relative electron transport rate (rETRmax) significantly differed between salinities of 28 and 18. Chlorophyll *a* and β-Carotene remained at high concentrations in all treatments showing pronounced acclimation during the experiment. High mannitol concentrations were measured throughout the experiment, while phlorotannins were high at low salinity. Hyposalinity and light are interacting drivers of the physiological and biochemical acclimation process for *D. aculeata*. Our experiment highlights the high ecophysiological plasticity of *D. aculeata*, suggesting that the species will likely be capable of withstanding future habitat changes in the Arctic.

Keywords: Arctic; mannitol; acclimation; F_v/F_m; pigments

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1. Introduction

Global warming generates a series of changes in Arctic marine biota, also strongly affecting the Svalbard Archipelago [1]. Marine benthic communities are constantly interacting with changes in environmental factors, especially in the intertidal zone. Increasing temperatures in the surface waters of Arctic fjords [2] result in changes in the thickness and extent of sea ice [3]. Furthermore, elevated atmospheric temperatures will increase the meltwater inflow to the fjords, altering both salinity and irradiance conditions in the water column [4]. These changes directly affect marine benthic communities, which have long been the focus of studies in Kongsfjorden, Svalbard [5]. There, habitat-providing ecosystem engineers, such as marine seaweeds, are of high ecological importance [6,7] and are key primary producers [8]. More than 197 species of seaweed have been described for the Svalbard region [9]. Among them, the brown alga *Desmarestia aculeata* has been shown to host a particularly diverse associated fauna comprised of 36 invertebrate species [6].

There are four possible responses of benthic communities to environmental perturbations: acclimation, adaptation, migration or death [10,11]. Therefore, only species with high ecophysiological plasticity are likely to prevail in shifting marine environments. *Desmarestia aculeata* can adjust pigmentation and photosynthetic responses to pronounced environmental variation throughout the summer period in Kongsfjorden, decreasing chlorophyll *a* concentration in the months of highest irradiance [12,13] *D. aculeata* has a wide distribution in the North Atlantic [14], even extensively inhabiting the Arctic coastal zone [15,16]. It is frequently found in association with its congener species *D. viridis* [17,18]. The species is also commonly found attached to rocks and as an epiphyte on other brown seaweeds, such as *Saccharina latissima* or *Laminaria hyperborea* [19,20], and forms extensive submarine meadows in the shallow subtidal and intertidal zones during the summer [17].

Previous studies in *D. aculeata* have described the lack of gene regulation under variations in temperature and carbon dioxide (CO_2) levels [21], presumably resulting in high energy costs for maintenance. Furthermore, nutrient assimilation does not seem to be affected by nutrient enrichment during the summer season, thus presenting a plastic response towards this factor [22]. The effect of irradiance and temperature, and the interaction between these factors, on photosynthetic parameters (α, rETRmax or *E*k) and biochemical analysis (pigment and antioxidant analysis) has been previously reported for *D. aculeata* [12,23,24]. In this context, temperature defines the distribution range of *D. aculeata*, due to its wide tolerance range of 0–20 °C [25]. The effect of other factors, such as hyposalinity, has been previously described as having negative effects on algae, e.g., *P. palmata* [26] or *Alaria esculenta* [27]. However, other species, such as *Laminaria digitata* or *L. solidungula*, show a high tolerance to hyposaline conditions [28]. In general, few studies have tested the acclimation responses of *D. aculeata* to multiple, and presumably interacting, abiotic factors, particularly to those relevant under climate change scenarios. Such assessment is essential to predict the performance of this species of high ecological relevance in Arctic fjord systems.

Hence, this study aims to explore the effect of interacting environmental drivers relevant to the habitat of the brown seaweed *D. aculeata*, specifically salinity fluctuations and light cycles (irradiance) at low temperatures. In addition, the study will contribute to our understanding of the limits of physiological tolerance of *D. aculeata* from the Arctic in a scenario of climate change.

2. Materials and Methods

2.1. Collection of Algal Material

This experiment was conducted at Kings Bay Marine Laboratory, Ny-Ålesund, Kongsfjorden, Spitsbergen-Svalbard in July 2019. Samples of the brown seaweed *Desmarestia aculeata* were collected in the intertidal zone at low tide in front of the marine laboratory (78°55′39.8″ N; 11°55′48.3″ E). The specimens were kept in seawater while they were cleaned from epiphytes and sediment. Subsequently, samples of algal tissue were collected from the frond.

2.2. Experimental Set-Up

The samples were kept in a pre-control treatment, for five days, in aerated 1 L tanks, at 0 °C with salinity (S_A) 34 seawater enriched with 1/2 Provasoli solution (1/2 PES, [29], modifications: HEPES-buffer instead of Tris, double the concentration of Na_2 glycerophosphate, iodine enrichment after [30]) and a constant irradiance of 50 µmol photons $m^{-2}s^{-1}$. After an acclimation period over 5 days, the experiment ran for 21 days. Therefore, the samples were pre-acclimatised to the control salinity S_A 34. For 21 days at the start of the experiment, a part of the samples was kept at the control S_A 34 and we proceeded to test the effects of hyposalinity at S_A 28 and 18. All treatments were maintained at 0 °C. To simulate the meltwater inflow from glacial run-off, the water in the experiment was diluted using fresh water [31]. The water was exchanged every fourth day throughout the experiment. Measurements and samples were taken on days 1 and 21.

Regarding the light intensity values, these are based on Kongsfjorden values during a daily cycle [32]. Irradiance was cycled every 12 h between the highest irradiance point at 500 µmol photons $m^{-2}s^{-1}$ (HL) and the lowest at 50 µmol photons $m^{-2}s^{-1}$ (LL). The light points were reached every 12 h, increasing hourly for 12 h until HL was reached and decreasing hourly for 12 h until LL was reached, making up the 24 h daily cyclic irradiance. Measurements were made specifically at 500 µmol photons $m^{-2}s^{-1}$ (HL) and at the 50 µmol photons $m^{-2}s^{-1}$ (LL) period. The configuration of the light cycles was carried out using the ProfiLux 3 system (with LED Mitras daylight, GHL Advanced Technology, Kaiserslautern, Germany).

After the measurements (see below Physiological parameters), the samples were shock-frozen in liquid nitrogen and stored at −80 °C. Afterward, the samples were freeze-dried for 24 h, the dry weight (DW) was obtained, and the biochemical analyses were performed.

2.3. Physiological Parameters

The maximum quantum yield of photosystem II (F_v/F_m) was measured in vivo after leaving the samples for 10 min in the dark. Subsequently, photosynthesis-irradiance (P-E) curves were recorded up to an irradiance of 600 µmol photons $m^{-2}s^{-1}$ to obtain the following parameters: photosynthetic capacity expressed as maximum relative electron transport rate (rETRmax), saturation irradiance (*E*k), and photosynthetic efficiency (α, initial linear slope). The (P-E) curves were fitted according to the equation of Platt et al. [33], using the program KaleidaGraph version 4.5.4 (Synergy Software, Reading, PA, USA). All analyses were performed using an amplitude-modulated chlorophyll fluorometer (Imaging PAM, Heinz Walz GmbH, Effeltrich, Germany).

2.4. Biochemical Parameters

Pigment analysis of *Desmarestia aculeata* was carried out following the methodology of Koch et al. [34] for brown seaweeds. Freeze-dried samples weighing 30 mg (n = 3) were measured using a high-performance liquid chromatography (HPLC) LaChromeElite system with a chilled L-2200 autosampler and an L-2450 DAD detector (VWR-Hitachi International GMBh, Darmstadt, Germany). Subsequently, using the methodology of Wright et al. [35], the following pigments were quantified: Chlorophyll *a* (Chl *a*), Chlorophyll *c2* (Chl *c2*), Fucoxanthin (Fucox), β-Carotene (β-Car), Violaxanthin (Viol), Antheraxanthin (Anthera) and Zeaxanthin (Zeax). Pigment content was finally expressed as µg g^{-1} (DW). Additionally, the xanthophyll cycle pool (VAZ: violaxanthin, antheraxanthin, zeaxanthin) and the de-epoxidation state (DPS) were calculated for *D. aculeata*.

The quantification of the content of the sugar alcohol mannitol in *Desmarestia aculeata* was carried out following the methodology proposed by Karsten et al. [36]. Freeze-dried samples weighing 10–15 mg were incubated in 1 mL of aqueous ethanol (70%, *v*/*v*) in a water bath at 70 °C for 4 h. Concentration determination was performed according to Diehl et al. [26]. D(-)-mannitol ($C_6H_{14}O_6$, Roth) standards of 1, 10, and 20 mM were used for calibration. The mannitol concentration was expressed in mg g^{-1} (DW).

For total carbon C (% DW), total nitrogen N (% DW), and C:N (%) ratio, 4–5 mg of freeze-dried sample (n = 3) sampled at days 1 and 21 of the *Desmarestia aculeata* culture were used. The measurement time of each sample was 150 s The samples were combusted at 1000 °C, acetanilide (C_8H_9NO) was used as standard, C and N samples were quantified using the Euro EA 3000 Elemental Analyser (Eurovector S.P.A., Milan, Italy). Total C and N concentrations were expressed in mg g^{-1} dry weight (DW). The C:N ratio (%) was obtained based on these results.

The concentration of phlorotannins in *D. aculeata* was measured using the Folin-Ciocalteu method described by Cruces et al. [37]. Purified phloroglucinol (Sigma-Aldrich) was used as standard. Freeze-dried samples of 20 mg (n = 3) were used for extraction and quantification. One millilitre of acetone (70%, *v*/*v*) was added to each sample and subsequently kept at 4 °C for 24 h in the dark. Absorbance was measured at λ = 730 nm using a microplate spectrophotometer. Finally, the quantification of total soluble phlorotannins was expressed in mg g^{-1} (DW).

2.5. Statistical Analysis

Statistical analyses were performed considering day 1 and 21 of culture. Tests for normal distribution (Shapiro-Wilk test; $p > 0.05$) were performed for all data sets. The data were $\log_{10}$-transformed where necessary. Three-way ANOVAs were then performed for each parameter measured. Tukey's post-hoc test was applied to detect significant differences ($p < 0.05$). This test was applied for each parameter analysed. Statistical analyses were run using RStudio (version 1.1.383, Boston, MA, USA).

3. Results

Regarding the photosynthetic parameters of *Desmarestia aculeata*, only a few clear impacts could be determined (Table 1). The rETRmax and α tended to decrease over time, while *E*k and the F_v/F_m remained almost unchanged. Even though significant differences regarding salinity were found for rETRmax and *E*k. Light had no major impact on the photosynthesis, however, significantly higher rETRmax, *E*k and F_v/F_m values were measured in the HL treatments, mainly at S_A 34 on day 1. Interestingly, different interactions between days, light and salinity were detected within all parameters, mainly in the parameters rETRmax, *E*k, and F_v/F_m (Table S1: Photosynthetic parameter).

Pigments were almost unaffected throughout the experiment and by the different treatments (Tables 2 and 3), and an interaction between days, light and salinity was only detected for fucoxanthin (Table S1: Pigments). Few significant differences in pigment concentrations were found for Chl *c2*, β-Car and Fucox, which, however, could not be directly assigned to the sampling day, high light (HL), low light (LL) or hyposalinity. The VAZ significantly decreased from day 1 to day 21 at S_A 34 and 28, and revealed lower concentrations in the HL treatments on day 1. Increases in the DPS were only determined when comparing day 1 and 21 at S_A 34 and 28. No differences were found for the light and salinity treatments.

Mannitol (Figure 1a) neither changed over time nor was affected by light or salinity. However, significant interactions between light and salinity were found (Table S1: Sugar Alcohol). Overall, high mannitol values were recorded in all samples during the experiment (Figure 1a). Significantly higher phlorotannin concentrations were measured at lower salinities (S_A 28 and 18) and the content increased over time (Figure 1b). Regarding the different light treatments, no significant differences between HL and LL were detected, except for the samples from day 21 at S_A 34.

Table 1. Photosynthetic parameters of *Desmarestia aculeata*: rETRmax, α, *E*k, and F_v/F_m. Experimental set-up: salinity (S_A)–Light (L) (High Light (HL)–Low Light (LL)) treatments. Values are means ± SD (n = 3). For each parameter (L, Days, S_A), statistically significant differences are marked by different lowercase letters. For all the data, three-way ANOVA with post-hoc Tukey's test was performed ($p < 0.05$).

S_A	Days	L	rETRmax (rel. Units)	Significance L	Days	S_A	α (µmol Photons $m^{-2}s^{-1})^{-1}$	Significance L	Days	S_A	*E*k (µmol Photons $m^{-2}s^{-1}$)	Significance L	Days	S_A	F_v/F_m (rel. Units)	Significance L	Days	S_A
34	1	HL	31.360 (±2.05)	a	a	ab	0.202 (±0.01)	a	a	a	156.473 (±22.28)	a	a	a	0.618 (±0.01)	a	a	a
		LL	20.183 (±2.78)	b			0.213 (±0.01)	a			94.597 (±8.38)	b			0.427 (±0.10)	b		
	21	HL	13.130 (±1.77)	a	b		0.193 (±0.02)	a	a		69.221 (±17.52)	a	b		0.399 (±0.10)	a	a	
		LL	12.893 (±1.25)	a			0.229 (±0.02)	a			56.430 (±6.35)	a			0.532 (±0.02)	a		
28	1	HL	18.557 (±3.12)	a	a	a	0.235 (±0.03)	a	a	a	79.370 (±12.64)	a	a	b	0.613 (±0.06)	a	a	a
		LL	20.656 (±2.12)	a			0.256 (±0.02)	a			80.903 (±7.68)	a			0.590 (±0.06)	a		
	21	HL	13.046 (±0.52)	a	b		0.202 (±0.02)	a	b		64.996 (±7.43)	a	a		0.511 (±0.03)	a	a	
		LL	14.239 (±2.14)	a			0.187 (±0.02)	a			76.627 (±14.93)	a			0.394 (±0.04)	b		
18	1	HL	22.529 (±3.42)	a	a	b	0.233 (±0.02)	a	a	a	97.819 (±22.09)	a	a	a	0.498 (±0.11)	a	a	a
		LL	21.794 (±5.33)	a			0.201 (±0.04)	a			110.722 (±29.33)	a			0.359 (±0.05)	a		
	21	HL	20.863 (±4.95)	a	a		0.173 (±0.02)	a	b		120.807 (±24.36)	a	a		0.512 (±0.03)	a	a	
		LL	16.210 (±3.97)	a			0.178 (±0.02)	a			90.114 (±13.74)	a			0.532 (±0.03)	a		

Table 2. Concentration of main pigments [µg g^{-1} dry weight (DW)] of *Desmarestia aculeata*: Chl *a*, Chl *c2*, β-Car, Fucox. Experimental set-up: salinity (S_A)–Light (L) (High Light (HL)–Low Light (LL)) treatments. Values are means ± SD (n = 3). For each parameter (L, Days, S_A), statistically significant differences are marked by different lowercase letters. For all the data, three-way ANOVA with post-hoc Tukey's test was performed ($p < 0.05$).

S_A	Days	L	Chl *a* (µg g^{-1} DW)	Significance L	Days	S_A	Chl *c2* (µg g^{-1} DW)	Significance L	Days	S_A	β-Car (µg g^{-1} DW)	Significance L	Days	S_A	Fucox (µg g^{-1} DW)	Significance LL	Days	S_A
34	1	HL	478.73 (±61.74)	a	a	a	60.60 (±15.42)	a	a	ab	21.03 (±4.32)	a	a	a	178.83 (±6.48)	a	a	a
		LL	450.60 (±44.34)	a			51.07 (±5.52)	a			17.07 (±3.76)	a			192.60 (±6.24)	a		
	21	HL	447.53 (±51.20)	a	a		58.10 (±9.40)	a	a		18.10 (±2.07)	a	a		203.63 (±27.75)	a	a	
		LL	328.70 (±41.66)	a			87.73 (± 3.25)	a			12.03 (±1.68)	a			140.93 (±28.62)	a		

Table 2. *Cont.*

S_A	Days	L	Chl *a* ($\mu g\ g^{-1}$ DW)	Significance L	Days	S_A	Chl *c2* ($\mu g\ g^{-1}$ DW)	Significance L	Days	S_A	β-Car ($\mu g\ g^{-1}$ DW)	Significance L	Days	S_A	Fucox ($\mu g\ g^{-1}$ DW)	Significance LL	Days	S_A
28	1	HL	526.90 (±144.48)	a	a	a	85.60 (±11.82)	a	a	a	19.57 (±5.86)	a	a	a	177.47 (±9.46)	a	a	a
		LL	536.83 (±192.22)	a			62.53 (±4.83)	a			21.10 (±7.95)	a			144.10 (±1.73)	a		
	21	HL	394.53 (±74.28)	a	a		53.87(±14.77)	a	a		11.37 (±2.94)	a	b		183.17 (±43.07)	a	a	
		LL	391.57 (±33.67)	a			70.63 (±3.40)	a			11.07 (±0.67)	a			163.97 (±13.98)	a		
18	1	HL	454.47 (±111.25)	a	a	a	68.80 (±2.51)	a	a	b	16.03 (±1.44)	a	a	a	167.43 (±6.82)	a	a	a
		LL	405.10 (±12.87)	a			48.37 (±2.32)	b			15.17 (±1.22)	a			165.27 (±2.25)	a		
	21	HL	334.97 (±43.70)	a	a		39.37 (±5.89)	a	a		15.10 (±0.50)	a	a		140.03 (±20.06)	a	a	
		LL	472.90 (±33.20)	a			76.77 (±6.62)	b			11.00 (±3.80)	a			228.37 (±15.87)	b		

Table 3. The pool of the xanthophyll cycle—VAZ ($\mu g\ g^{-1}$ dry weight (DW)) and de-epoxidation state (DPS). Experimental set–up: salinity (S_A)–Light (L) (High Light (HL)–Low Light (LL)) treatments of *Desmarestia aculeata*. Values are means ± SD (n = 3). For each parameter (L, Days, S_A), statistically significant differences are marked by different lowercase letters. For all the data, three-way ANOVA with post-hoc Tukey's test was performed ($p < 0.05$).

S_A	Days	L	VAZ ($\mu g\ g^{-1}$ DW)	Significance L	Days	S_A	DPS	Significance L	Days	S_A
34	1	HL	0.35 (±0.03)	a	a	a	1.58 (±0.12)	a	a	a
		LL	0.27 (±0.04)	a			1.95 (±0.28)	a		
	21	HL	0.26 (±0.02)	a	b		2.16 (±0.07)	a	b	
		LL	0.21 (±0.03)	a			2.70 (±0.32)	a		
28	1	HL	0.40 (±0.06)	a	a	a	1.48 (±0.26)	a	a	a
		LL	0.29 (±0.08)	b			2.01 (±0.66)	a		
	21	HL	0.23 (±0.04)	a	b		2.44 (±0.37)	a	b	
		LL	0.19 (±0.04)	a			2.82 (±0.41)	a		
18	1	HL	0.29 (±0.02)	a	a	a	1.83 (±0.15)	a	a	a
		LL	0.24 (±0.02)	b			2.26 (±0.17)	a		
	21	HL	0.22 (±0.03)	a	a		2.52 (±0.31)	a	a	
		LL	0.26 (±0.01)	a			2.17 (±0.13)	a		

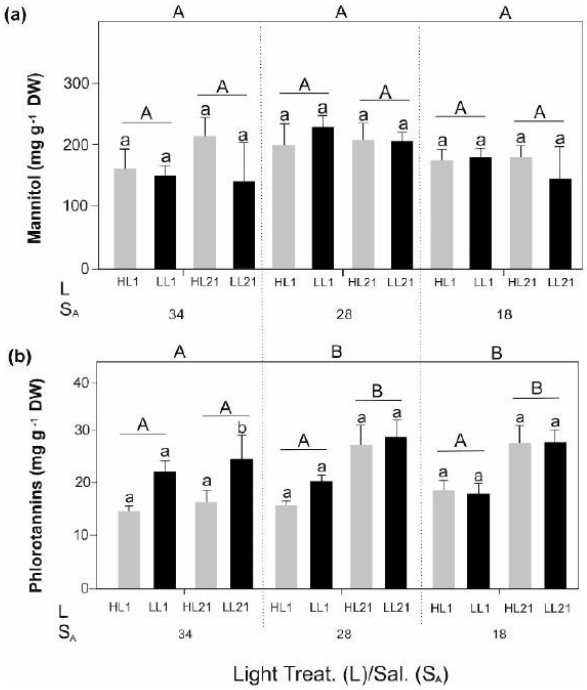

Figure 1. Concentration in mg g^{-1} dry weight (DW) for compounds in *Desmarestia aculeata*: (**a**) Mannitol; (**b**) Phlorotannins. Experimental set-up: salinity (S_A)–Light (L) (High Light (HL)–Low Light (LL)) treatments. Values are means ± SD (n = 3). Statistically significant differences between HL and LL per treatments are marked by different lowercase letters. Statistically significant differences between treatment days (1–21) are marked by different uppercase letters and differences between salinities (S_A 34, 28, and 18) are marked by different uppercase letters outside the graph. For all the data, three-way ANOVA with post-hoc Tukey's test was performed ($p < 0.05$).

The total carbon (C) content remained completely unchanged throughout the experiment (Figure 2b). Similarly, total nitrogen (N) showed no significant differences with light or salinity (Figure 2a). However, total N significantly changed over time; there was no trend towards higher or lower concentrations. The C:N ratio did not reveal clear effects in the different treatments (Figure 2c). Over time, higher C:N ratios were only found at S_A 28 and the significant impact by salinity could not be assigned to the absolute salinities in general. Significantly lower total N at S_A 28 and HL on days 21 resulted in significantly higher C:N ratios in the same samples. However, total N, total C and the C:N ratio exhibited days:light:salinity interactions (Table S1: Total Contents).

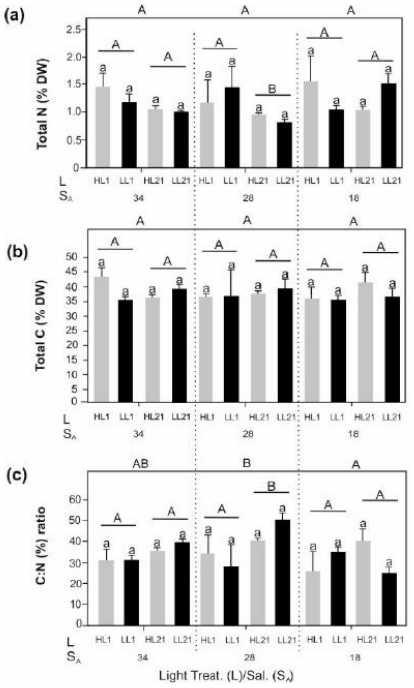

Figure 2. Elemental composition of *Desmarestia aculeata* at days 1 and 21 of treatment. (**a**) Contents of total N (% DW); (**b**) Contents of total C (% DW); (**c**) C:N ratio. Experimental set–up: salinity (S_A)—Light (L) (High Light (HL)–Low Light (LL)) treatments. Values are means ± SD (n = 3). Statistically significant differences between HL and LL per treatments are marked by different lowercase letters. Statistically significant differences between treatment days (1–21) are marked by different uppercase letters and differences between salinities (S_A 34, 28, and 18) are marked by different uppercase letters outside the graph. For all the data, three-way ANOVA with post-hoc Tukey's test was performed ($p < 0.05$).

4. Discussion

In this study, physiological and biochemical acclimation processes of the brown seaweed *Desmarestia aculeata* were evaluated after simulating different salinity conditions and diurnal changes in irradiance. The tested environmental parameters and time were observed to mainly have an impact on the photosynthetic responses of *D. aculeata*, while biochemical acclimation was less pronounced. The observed strong interactive effects of light, salinity and time highlight the complex interplay of the various environmental factors affecting the species.

Salinity variation, as a consequence of increased meltwater discharge to Arctic fjords, has been widely described as a direct effect of climate change [38,39]. It has been observed that decreasing salinity in the first few meters of the water column directly affects photosynthetic performance in polar brown algae [26,27,40]. However, in addition to such changes occurring by global warming, diurnal variation in irradiance represents an additional stress factor for seaweeds. Hanelt et al. [41,42] described how fluctuations in daily irradiance levels during the Arctic summer affect internal photosynthetic and biochemical regulation in seaweeds. Hence, brown seaweeds inhabiting the shallow subtidal zone are constantly exposed to marked variations in salinity and irradiance levels. Our study revealed the resilience of the species *D. aculeata* to environmental changes, namely changes in salinity and irradiance, facilitated by a high plasticity of its internal regulation.

This high tolerance of certain brown seaweeds to varying salinity agrees with what was recorded in our experiment. The F_v/F_m of *D. aculeata* was not diminished by decreasing salinities. However, other photosynthetic parameters such as rETRmax and *E*k showed clear responses to low salinities of S_A 28 and 18, respectively. The variations of rETRmax and *E*k show how this species is able to regulate its photosynthetic activity and ensure that the maximal quantum yield of PSII is maintained at high values. Irradiance plays a fundamental role in the photosynthetic processes of seaweeds [43]. However, during our experiment, the photosynthetic variables of *D. aculeata* were not generally affected by variations in the daily course of irradiance. The fact that both high light (HL) and low light (LL) had no major effect highlights the high plasticity of *D. aculeata* to a fluctuating light climate, given by its ability for internal regulation. This observation differs from the high sensitivity described for *D. aculeata* under constant light intensities. Marambio and Bischof [24] described how high constant irradiance affects the photosynthetic parameters of *D. aculeata*, such as F_v/F_m, rETRmax, α, and *E*k, over time. F_v/F_m has been observed to decrease during periods of high irradiance, for example in *L. digitata* and *Saccharina latissima* [44,45] or *Chondrus crispus* analysed under natural and laboratory conditions [46]. All these species showed a high acclimation to daily cyclic variations in irradiance.

Regarding pigments, we observed that Chl *a* and β-Car in *D. aculeata* were neither affected by high nor low daily irradiance, or by low salinity. On the other hand, the accessory pigments Chl *c2* and Fucox apparently have a crucial role as photosynthetic regulators: under the variation of daily cyclic irradiance, these two pigments showed a high acclimation to HL and LL during the experiment at high and low salinity, but VAZ and DPS were not affected by the low salinities S_A 28 and 18. This is contrary to what has been observed in other species, such as *S. latissima*, which in laboratory culture has been shown to be strongly affected by the low salinity [47].

Mannitol is part of carbon storage in the photosynthetic process in brown seaweeds [48]. Additionally, this photosynthetic product acts as protectant against osmotic stress [49,50]. However, during our experiment, we did not find any effect of salinity or irradiance on the mannitol concentration in *D. aculeata* during the 21 days of treatment. Still, high concentrations were observed throughout all treatments. On the one hand, constant high mannitol content could be an acclimation to the frequently experienced environmental fluctuations in the intertidal zone, where *D. aculeata* was collected. On the other hand, we suspect that the high concentrations are an additional thermal protection mechanism of *D. aculeata*, since mannitol can also act as an anti-freezing compound [51]. As reported by Monteiro et al. [52], the brown alga *S. latissima* also reaches concentrations of approximately 200 mg g^{-1} DW at S_A 30 and 0 °C, which is in agreement with what was measured in our study. However, the effect of low temperature on *D. aculeata* was not specifically evaluated during our experiment.

Phlorotannins, another important group of brown algal compounds, have been described as contributing to the reinforcement of cell walls under hyposaline conditions, e.g., in the brown alga *Alaria esculenta* [53]. In addition, phlorotannins are actively involved in protection against intense irradiance, and protection of tissues against pathogenic microbial activity and herbivory [54–56]. For *D. aculeata*, high phlorotannin values were observed at all salinities tested in this experiment. Our results are in agreement with those described by Springer et al. [53] for *A. esculenta* at different salinity levels and with those observed by Ragan & Jensen [57] for *Fucus vesiculosus* during winter with low temperatures. Although the content of phlorotannins is overall high, a variation in concentration was observed at S_A 34 under daily cycles of irradiance. Importantly, phlorotannins may be activated depending on conditions and move through the cell wall to increase their site-specific content [53,58]. It remains unresolved whether the response of phlorotannins to S_A 28 and 18 on day 21 of cultivation is a driver-specific or a non-specific response of the seaweed to non-favourable conditions.

In contrast to previous studies on *L. solidungula* [34] and *F. serratus* [59] from Spitsbergen, total N and the C:N ratio of *D. aculeata* were not affected by salinity variations. Samples

were also not affected by HL and LL. However, even though the samples were maintained at $\frac{1}{2}$ PES, all treatments revealed C:N ratios higher than 20, indicating N limitation [60]. The uptake and assimilation of nutrients are known to be impacted by temperature-changing enzymatic processes [61]. It is possible that N limitation was caused by reduced N uptake potential due to the slowed enzymatic action at 0 °C.

5. Conclusions

The response of this population of *D. aculeata* revealed a high potential for acclimation to the different environmental parameters to which it was exposed to. In our experiment, *D. aculeata* responded rapidly through metabolic regulation to cyclic light variations and was not affected by the hyposaline condition. As previously mentioned, the *D. aculeata* population studied inhabits the intertidal and upper subtidal zone and is therefore constantly exposed to a highly dynamic abiotic environment, including exposure to meltwater (field observation). This could explain the high plasticity of this population of *D. aculeata* to low salinity and large fluctuations in irradiance. The reaction of photosynthetic and biochemical parameters of *D. aculeata* to different factors shows how this phenotype can cope with change in multiple drivers. This mechanism is key to generating resistance through a rapid and effective acclimation process [40,62].

Ecologically, *D. aculeata* is not a strictly polar seaweed; its life history as a temperate-boreal species gives it a unique characteristic, and it is distributed over a wide geographical range. Therefore, future changes in the habitat of this species will be determined by the intensity and duration of climate change events. Our data support that this population of *D. aculeata* will be able to quickly adjust to changing environmental conditions in the Arctic coastal zone due to its high ecophysiological plasticity. Finally, through the study of this population, it was possible to obtain important information about the resilience of these *D. aculeata* individuals, in order to predict future responses to environmental changes.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/biology11101499/s1. Table S1: Results of three-way ANOVA for *Desmarestia aculeata*.

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Supplementary Table 1.

Results of three-way ANOVA for *Desmarestia aculeata* (n=3): effects of the daily cyclic irradiance and salinities. Photosynthetic parameters (F_v/F_m, α, *E*k, and rETRmax); Pigments (Chl *a*, Chl *c2*, β-Car, Fucox, VAZ, and DPS); Total elemental contents (C %, N %, and C:N ratio %); Phlorotannins; Mannitol. Non-parametric data were transformed and are marked by (•). Asterisks (*) indicate statistically significant values: (***) p<0.001, (**) p<0.01, and (*) p<0.05.

	Variable	Factor	*df*	*F*-value	*p*-value	
Photosynthetic parameter	rETRmax	Days	1	51.620	<0.001	***
		Light	1	4.716	0.040	*
		Salinity	2	4.639	0.020	*
		Days:Light	1	0.967	0.335	
		Days:Salinity	2	6.982	0.004	**
		Light:Salinity	2	4.237	0.027	*
		Days:Light:Salinity	2	4.783	0.018	*
	*E*k	Days	1	17.007	<0.001	***
		Light	1	5.326	0.030	*
		Salinity	2	9.000	0.001	**
		Days:Light	1	0.206	0.654	
		Days:Salinity	2	11.933	<0.001	***
		Light:Salinity	2	5.044	0.015	*
		Days:Light:Salinity	2	5.503	0.011	*
	α	Days	1	15.524	<0.001	***
		Light	1	0.347	0.561	
		Salinity	2	3.300	0.054	
		Days:Light	1	0.352	0.558	
		Days:Salinity	2	5.101	0.014	*

		Light:Salinity	2	1.979	0.160	
		Days:Light:Salinity	2	2.282	0.124	
	F_v/F_m	Days	1	3.283	0.083	
		Light	1	6.512	0.018	*
		Salinity	2	2.132	0.141	
		Days:Light	1	9.735	0.005	**
		Days:Salinity	2	11.617	<0.001	***
		Light:Salinity	2	0.360	0.702	
		Days:Light:Salinity	2	8.615	0.002	**
Pigments	Chl *a*	Days	1	3.215	0.058	
		Light	1	0.088	0.769	
		Salinity	2	0.924	0.411	
		Days:Light	1	0.233	0.624	
		Days:Salinity	2	1.278	0.297	
		Light:Salinity	2	1.428	0.260	
		Days:Light:Salinity	2	2.053	0.150	
	Chl *c2*	Days	1	3.341	0.080	
		Light	1	0.319	0.578	
		Salinity	2	4.168	0.028	*
		Days:Light	1	66.083	<0.001	***
		Days:Salinity	2	2.203	0.132	
		Light:Salinity	2	8.984	0.001	**
		Days:Light:Salinity	2	1.187	0.322	
	β-Car	Days	1	17.822	<0.001	***
		Light	1	3.448	0.076	
		Salinity	2	1.633	0.216	
		Days:Light	1	0.934	0.343	
		Days:Salinity	2	2.602	0.095	
		Light:Salinity	2	1.738	0.197	
		Days:Light:Salinity	2	0.030	0.970	
	Fucox	Days	1	0.786	0.384	
		Light	1	0.156	0.696	
		Salinity	2	0.165	0.329	
		Days:Light	1	0.528	0.475	
		Days:Salinity	2	2.246	0.128	
		Light:Salinity	2	12.451	<0.001	***
		Days:Light:Salinity	2	13.914	<0.001	***

	VAZ	Days	1	31.556	<0.001	***
		Light	1	13.284	0.001	**
		Salinity	2	1.216	0.314	
		Days:Light	1	5.056	0.340	*
		Days:Salinity	2	5.300	0.124	*
		Light:Salinity	2	2.709	0.087	
		Days:Light:Salinity	2	0.472	0.630	
	DPS	Days	1	35.310	<0.001	***
		Light	1	3.256	0.054	
		Salinity	2	0.356	0.704	
		Days:Light	1	1.394	0.249	
		Days:Salinity	2	2.667	0.090	
		Light:Salinity	2	1.813	0.185	
		Days:Light:Salinity	2	1.840	0.181	
Sugar Alcohol	Mannitol•	Days	1	0.845	0.367	
		Light	1	0.136	0.715	
		Salinity	2	0.226	0.799	
		Days:Light	1	0.113	0.739	
		Days:Salinity	2	0.536	0.592	
		Light:Salinity	2	7.914	0.002	**
		Days:Light:Salinity	2	3.381	0.051	
Phlorotannins	Phloro•	Days	1	64.722	<0.001	***
		Light	1	16.132	<0.001	***
		Salinity	2	6.828	0.004	**
		Days:Light	1	0.038	0.847	
		Days:Salinity	2	8.537	0.002	**
		Light:Salinity	2	6.386	0.006	**
		Days:Light:Salinity	2	0.569	0.573	
Total Contents	N (%)•	Days	1	12.742	0.002	**
		Light	1	0.385	0.541	
		Salinity	2	3.215	0.058	
		Days:Light	1	2.346	0.139	
		Days:Salinity	2	3.710	0.039	*
		Light:Salinity	2	0.547	0.586	
		Days:Light:Salinity	2	8.760	0.001	**
	C (%)•	Days	1	0.748	0.396	

	Light	1	1.575	0.222	
	Salinity	2	0.422	0.661	
	Days:Light	1	1.203	0.284	
	Days:Salinity	2	1.744	0.196	
	Light:Salinity	2	1.315	0.287	
	Days:Light:Salinity	2	4.013	0.031	*
C:N (%)	Days	1	15.109	<0.001	***
	Light	1	0.010	0.920	
	Salinity	2	3.649	0.041	*
	Days:Light	1	0.178	0.677	
	Days:Salinity	2	2.971	0.070	
	Light:Salinity	2	0.641	0.536	
	Days:Light:Salinity	2	9.755	<0.001	***

(•) $\log_{10}$ transformation

7. Synoptic Discussion

7.1 *Ecophysiological response to interacting abiotic drivers (temperature, irradiance and salinity) in Arctic seaweeds*

Environmental variables may change simultaneously and rapidly, causing drivers to act independently or in combination (Fredersdorf et al. 2009). Factors such as irradiance, temperature, and salinity are drivers that directly affect algal ecophysiology (Hanelt et al. 2003; Schmedes & Nielsen 2020). Only few studies so far have focused on the interactive effects of abiotic factors on Arctic seaweed. Some of them are: salinity and temperature in *Laminaria solindungula* and *Saccharina latissima* (Diehl et al. 2020; Li et al. 2020; Monteiro et al. 2021), salinity, temperature and radiation in *Alaria esculenta* (Fredersdorf et al. 2009), salinity and UV in *Palmaria palmata* and *Devaleraea ramentacea* (Karsten et al. 2003), among others.

High irradiance is an abiotic factor with the potential to significantly stress photosynthetic organisms, forcing them to apply a range of photoprotective mechanisms to cope with it. In **publication I**, the species *Desmarestia aculeata* was shown to be affected by high irradiance at all temperatures studied. The negative effect of high irradiance has previously been observed in representatives of the order Desmarestiales (Chapman & Burrows 1970; Kain 1989; Gómez et al. 2009; Heinrich 2016; Savaglia et al. 2019). In Antarctic species such as *D. menziesii* and *D. anceps*, it has been observed that already at 100 μmol photons m^{-2} s^{-1}, there is a decrease in F_v/F_m, and an increase in rETR and *E*k values (Savaglia et al. 2019). It should be noted that *D. aculeata*, inhabits the North Atlantic and Arctic region. In the latter region, specimens show high photosynthetic efficiency, indicative for shade adaptation and a common feature in polar algae, which need high photosynthetic efficiency to cope with the low light environment (Chapman & Burrows 1970; Wiencke et al. 2009). On the other hand, in the presence of high irradiance a low photosynthetic efficiency was recorded in *D. aculeata*. This species shows that it is possible to regulate photosynthetic activity, in order to avoid the process of photoinhibition **(Publication I)**. Still, the combination of drivers could modulate light responses and, consequently, become a potent stressor in algae (Becker et al. 2009; Hurd et al. 2014): In **publications I** and **III**, *D. aculeata*, exhibited a synergistic response to the interaction of abiotic factors. *D. aculeata* was affected by temperature and irradiance in **publication I**, resulting in a decrease in Fucox and β-Car at high irradiance,

while VAZ tended to decrease at high temperature. In plants, low VAZ values have been observed in the presence of low irradiance

(García-Plazaola et al. 2002). On the other hand, contrary to what has been observed for temperature, in *D. aculeata* **(Publication I)**, Monteiro et al. (2021) describe how VAZ in *S. latissima* is unaffected by temperatures of 8 and 15 °C. Olischläger et al. (2017) mention how these mechanisms are part of the photoprotection process to avoid oxidative stress and are therefore important in regulating the internal energy flow of photosystems. *D. aculeata*, as shown in **publication I**, was able to have an effective acclimation process to temperature and irradiance variations.

However, *D. aculeata* can react in different ways when exposed to different abiotic factors. In **publication III**, it was observed that this species did not show reductions in F_v/F_m due to variations in salinity or irradiance. In **publication I**, at constant high irradiance *D. aculeata* showed negative effects on its photosynthetic parameters, while in **publication III**, it is able to regulate photosynthetic activity during irradiance cycles. For the study reported in **publication III**, *D. aculeata* was collected in the intertidal zone, and *E*k was observed to be high above 50 µmol photons m^{-2} s^{-1} in all treatments. This is consistent with that described by Wiencke et al. (2009) for seaweeds inhabiting the intertidal or shallow subtidal. At low salinity, the rETRmax of *D. acuelata* in **publication III** decreases, which is supported by increased levels of phlorotannins at low salinity, which could allow for a strategy of rapid acclimation to osmotic stress. In the studies to **publication III**, at the pigment level, no variation was observed with respect to salinity, which may be related to the stress of the daily irradiance cycle. The absence of any effect of salinity on *D. aculeata* in **publication III** differs from that proposed by Li et al. (2020), who described how *S. latissima* is affected physiologically and biochemically, causing a decrease in xanthophyll concentration in presence of moderate hyposaline conditions of S_A 20.

On the other hand, the red seaweed *P. palmata* in **publication I**, showed how the parameters F_v/F_m, α, and *E*k were affected by high irradiance. Our study agrees with the observations by Gómez et al. (2009), who describe how the Antarctic species *P. decipiens* in natural conditions show low *E*k values characteristic of deep habitat species. Hanelt et al. (2003), described how *P. palmata* in culture is sensitive to high irradiance, being light saturated at 100 µmol photons m^{-2} s^{-1}. In the study presented in **publication II**, *P. palmata* also showed low *E*k values, generally decreasing further at high PAR values. This is in agreement with Gómez & Huovinen (2011), who recorded low *E*k values between 100-150 µmol photons m^{-2} s^{-1} in seaweeds constantly exposed to high irradiance (1500 µmol photons m^{-2} s^{-1} at low tide

and 550 µmol photons m^{-2} s^{-1} at high tide) in the field, however, this study was conducted on seaweeds inhabiting the intertidal and shallow subtidal in Chile. Resultant from the impact of high irradiance and secondary factors the production of reactive oxygen species (ROS) could be initiated (Bischof & Rautenberger 2012), acting mainly as a mediator of cellular damage (Mackerness et al. 2001). The high level of stress produced by high irradiance in *P. palmata* during this study is supported by the decrease in PC and PE values at high irradiance. The decrease in PE is in agreement with that described by Sagert et al. (1997) for the same species, which concentration decreases due to adaptation to high irradiance. On the other hand, rETRmax and β-Car in *P. palmata* tend to show a synergistic response to irradiance and temperature **(Publication I)**. As indicator of dynamic photoinhibition in *P. palmata* **(Publication I)** a decrease in F_v/F_m and a high concentration of β-Car was observed in presence of high irradiance and temperature. Dynamic photoinhibition is characterised as a reversible process that can decrease F_v/F_m in the presence of high irradiance, generating energy dissipation which is regulated by carotenoids, in order to avoid chronic photoinhibition (Hanelt 1998, 2003). Results presented in **publication I** suggests that both species have a physiological capacity that is mainly regulated by irradiance.

On the other hand, *P. palmata* is markedly affected by hyposaline conditions **(Publication II)**, which is in agreement with the observations of Karsten et al. (2003), in which this species at S_A 15 showed a decrease in F_v/F_m and pigment loss. However, ecotypes of *P. palmata*, inhabit lower latitudes near to the coast of Kattegat, and can inhabit hyposaline zones, provided that the nutrient concentration is high (Schmedes & Nielsen 2020). In **publication II**, it was observed that the photosynthetic and biochemical regulatory capacity of *P. palmata* to daily irradiance cycles was affected by hyposalinity conditions at S_A 18. High NPQ values showed a rapid acclimation of *P. palmata* to irradiance variations during the daily cycle **(Publication II)**, which is in agreement with what was described by Runcie & Riddle (2006) in *Iridaea mawsonii*, which shows high NPQ values at high irradiances. However, NPQ values reported in **publication II** were affected by salinity, causing that *P. palmata* react more slowly to variations in irradiance during the daily cycle. The effect of low salinity on *P. palmata* is accompanied by a decrease in Chl *a* at S_A 18 and a tendency for Zeax and antioxidant activity to increase at high irradiance at S_A 18 **(Publication II)**; the increase of Zeax at high irradiance in *P. palmata* indicates a short-term acclimation process to daily irradiance variations, a process that becomes more complex under hyposaline conditions. Consequently, *P. palmata* **(Publication II)**, showed a limited physiological ability to acclimatise to hyposalinity conditions.

In **publication II**, the presence of secondary factors such as salinity directly affected the photosynthetic regulatory capacity against irradiance, demonstrating how one driver can prevail over another. Under the interaction of abiotic factors such as temperature, irradiance and salinity, *D. aculeata* **(Publication I, and III)** and *P. palmata* **(Publication I, and II)**, generated a response in relation to the strongest stressor. It has been described that the presence of an additional stressor is able to modify the effects of the initial factor in unknown directions Alexieva et al. (2003).

7.2 *Hyposalinity - a limiting condition to seaweeds in Arctic fjord systems?*

The coastline of the Svalbard archipelago is mainly influenced by regional conditions, such as topography, geography and ocean currents (Pavlova et al. 2019). The west coast of the archipelago receives warmer and saltier waters from the Atlantic, while the east coast has cooler and less saline waters of Arctic origin (Svendsen et al. 2002). On the other hand, the inner fjords of the Svalbard archipelago are influenced by marine and land-based glaciers, in addition to being influenced by the WSC, with warm, saline water from the Atlantic (Cottier et al. 2007). The increase in temperature of the WSC over the last decade has caused the inflow into the fjord to directly affect sea ice formation and thus lead to warming of the fjords in western Svalbard, *e.g*., Kongsfjorden (Cottier et al. 2007; Pavlov et al. 2013).

Due to the warming in the western fjords, an increase in glacial runoff and melting snow has been observed, generating hyposalinity conditions in the fjords (Hop et al. 2002). These variations in salinity ranges affect the ecophysiology of seaweeds. Some seaweeds species inhabiting Kongsfjorden, such as the brown seaweeds *Laminaria digitata* and *Fucus distichus*, do not show negative effects of hyposalinity on photosynthetic maximum quantum yield (F_v/F_m) and, hence, are shown to have a wide tolerance range between S_A 5 and 60 (Karsten et al. 2007). This finding coincides with what was observed for *Desmarestia aculeata* in **publication III**, where this species did not show variations in F_v/F_m in the presence of low salinity, showing its high tolerance under hyposalinity conditions and photosynthetic pigments such as Chl *a*, increased concentration by actively responding to decreased salinity. A high concentration of Chl *a* in higher plants and cyanobacteria of the genus *Synechocystis* has been associated with hyposaline and moderate salinity conditions, while in the presence of hypersalinity Chl *a* decreases (Schubert et al.1993; Sudhir & Murthy 2004; Taïbi et al. 2016).

It has been shown that *D. aculeata* at optimum salinity S_A 34, shows a high concentration of Chl *a* **(Publication I and III)** and also under hyposalinity conditions **(Publication III)**. VAZ and DPS values in *D. aculeata* were constant between salinity treatments, indicating that low salinity did not initiate the de-epoxidation process in pigments to avoid ROS generation **(Publication III)**. On the other hand, at the level of the early developmental stages, it is also possible to observe the effect of lower salinity, *e.g*., the zoospores of *Alaria esculenta* were studied at S_A 20, showing a decrease in photosynthetic activity, while in the adult stage at the same salinity, this species was not affected (Fredersdorf et al. 2009). However, adult sporophytes of Arctic seaweed such as *Saccharina latissima* are strongly affected by low salinities at S_A 5 and 10, or *Laminaria solindungula* at S_A 25, both species showing bleaching of fronds, decreased photosynthetic activity and direct effects on pigment and antioxidant concentration (Karsten et al. 2007; Diehl et al. 2020). As observed for *D. aculeata* in the studies to **publication III** this species would have no difficulty to inhabit the inner fjords and open water areas of western and eastern Svalbard.

Also, in red seaweed it has been observed that a decrease in salinity can have significant implications for the photosynthetic process (Larsen & Sand - Jensen 2006). Under hyposalinity conditions, *P. palmata* showed negative effects on its physiology, manifested by loss of pigment (bleaching of fronds) in **publication II**. The presence of bleaching in *P. palmata* is in agreement with the observations by Dummermuth (2003), who describes that at S_A 15, *P. palmata* loses its pigments and dies. In **publication II,** *Palmaria palmata*, presented a decrease in the F_v/F_m at S_A 28 and 18. Low F_v/F_m values, under hyposalinity conditions (S_A 28 and 20), have also been observed in *Alaria esculenta*, a boreal-Arctic brown algal species (Fredersdorf et al. 2009). With respect to photosynthetic pigments, *P. palmata* maintained generally high concentrations of Chl *a* and Lut under different salinity ranges **(Publication I and II)**. Notably in the results presented in **publication I**, Lut and Zeax were affected by low salinity possibly as part of the acclimation process of *P. palmata*. In the presence of stress, seaweeds exhibit various mechanisms, including the production of antioxidants as a means of cellular protection (Karsten et al. 2003; Dummermuth 2003). Under hyposalinity conditions, it has been observed that radical scavenging activity (DPPH) is increased in *P. palmata* **(Publication II)**. High DPPH activity is consistent with that observed in the red seaweed *Rhodymenia pseudopalmata* under low salinity conditions S_A 20 (Pliego - Cortés et al. 2017). Therefore, salinity obviously has a strong influence on the distribution of *P. palmata* **(Publication II)**. Although, this species has

a wide distribution in the North Atlantic and Arctic region, it is not able to inhabit areas with hyposaline conditions (Hill 2008; Schmedes & Nielsen 2020), being classified as a stenohaline seaweed (Dummermuth 2003). Because *P. palmata* is highly sensitive to salinity variations, its distribution within the fjords of the Svalbard archipelago may become increasingly limited. The effect of low salinity on this species may force it to migrate to deeper areas in Kongsfjorden. Also the presence of higher salinity in open water on the west side of Svalbard may suggest that the species may rather inhabit these coasts in the future, in search of more stable conditions.

7.3 *Simulating an Artic summer´s light regime and its implications on primary producers*

Seaweeds are also exposed to cyclic irradiance, which changes on a daily and seasonal based, and further influenced by tidal cycles. In the polar regions, irradiance is marked by strong seasonality, at 80 °N, summer lasts from mid-April to August, while winter is marked by darkness from October to February (Hanelt et al. 2003). As a consequence, seaweeds are exposed to strong irradiance and radiation as soon as the sea ice breaks up at the beginning of the Arctic summer (Bischof et al. 1999; Hanelt et al. 2001). In general, artificial sunlight produced in the laboratory is intended to simulate the natural light to which the organisms are exposed, but generally only comes close to natural conditions (Holm-Hansen et al. 1993). A great deal of work in macroalgal ecophysiology has been done on PAR light and the effects of excess light (Hanelt et al. 2003). Light regulates the photosynthetic activity of seaweeds living in the intertidal and upper subtidal zone (Hanelt et al. 2003; Hurd et al. 2014), but could also be one of the main abiotic stressors (Wiencke et al. 2006). In the face of stress, photosynthetic organisms such as seaweed develop photoprotective strategies, which consists of activating a series of regulatory mechanisms in order to minimise the damage caused by high irradiance (Carbonera et al. 2012). The marked seasonality in Arctic regions means that seaweeds living at high latitudes are strongly adapted to low-light/dark conditions (Amsler et al. 1995). Dark-adapted seaweeds have a high photosynthetic efficiency, which varies according to depth, deep-sea seaweeds have a low *E*k, while intertidal and upper subtidal seaweeds have a high *E*k (>50 umol) (Wiencke et al. 2009). In the North Atlantic and Arctic region, some works have focused on evaluating the effect of constant irradiance on seaweeds, *e.g.*, *Laminaria saccharina* (Hanelt et al. 1997), subarctic and Arctic Kelps (Krause-Jensen et al. 2016), *D. aculeata* and *P. palmata* **(Publication I)**, while others have studied the effect of cyclic diurnal or seasonal irradiance on seaweeds, *e.g.*, *D. aculeata* (López-Figueroa 1991), *P. palmata* (Sagert et al. 1997; 2000), *L. digitata*, *D. aculeata*, *P. palmata*, *Devaleraea ramentacea*

(Aguilera et al. 2002) and *D. aculeata* and *P. palmata* **(Publication II, and III)**, among others.

The Arctic summer is characterised by permanent daylight, however, irradiances are still lower compared to lower latitudes due to the low solar angle prevailing in the area. It should be noted that irradiance still varies over the course of 24 h during the Arctic summer. The permanent availability of light present during this time has strong implications for primary productivity (Wiencke et al. 2009). In the presence of high irradiance, the photosynthetic activity of seaweeds in the field decreases (Hanelt et al. 2003). The decrease in photosynthetic activity at constant high irradiance agrees with that observed for the species *D. aculeata* and *P. palmata* reported in **publication I**, which showed a decrease in their photosynthetic parameters. As an effect of the constant irradiance during the Arctic summer, algae can promote a continuous uptake of CO_2 (Krause-Jensen et al. 2016). In seasonal studies, it has been observed that the concentration of Chl *a* decreases in *P. palmata* during mid-summer and increases towards late summer (Aguilera et al. 2002; Bischof et al. 2002). The process of photoinhibition is frequent in seaweeds inhabiting the Arctic during the summer season. However, *P. palmata* can regulate its photosynthetic and biochemical activity seasonally, decreasing the possibility of photoinhibition (Aguilera et al. 2002).

During the daily irradiance cycle, the dynamic photoinhibition process has been observed to follow a diurnal pattern (Henley et al. 1991; Hanelt et al. 1993, 2003). This is in agreement with what was observed in **publication II** and **III**, where it was shown that *P. palmata* and *D. aculeata* are able to regulate their photosynthetic and biochemical activity during daily irradiance cycles. It should be noted that the process of photosynthetic regulation in high light is fragile and can be affected by other factors, *e.g.*, salinity **(Publication II)**. At high latitudes, the presence of constant light for 24 h in summer is an abiotic factor that directly influences the photosynthetic regulation of seaweeds. Peaks of high irradiance occur during the middle of the day, which also leads to increased stress levels in the seaweeds. Larkum & Barret (1983) describe how varying irradiance levels lead to a better management and distribution of energy within the photosystems of photosynthetic organisms; this management will be governed by excess energy dissipation mechanisms such as the xanthophyll cycle *e.g.*, in brown seaweeds or heat dissipation which may even involve the PSII reaction centre itself (Larkum et al. 2003). This is in agreement with what was observed in **publication I** and **III**, where pigments associated with the xanthophyll cycle and VAZ were mainly affected by cyclic or constant high irradiance. In the presence of hyposalinity, the xanthophyll cycle

continued to actively regulate the dissipation of excess energy in *D. aculeata* **(Publication III)**.

7.4 *Implications of climate changes to Arctic seaweeds*

Climatic conditions in the Arctic region are changing fast. Rapid warming has been observed in the Arctic and, as a result, melting of ice sheets, glaciers, and decreasing sea ice extent and thickness (Krause-Jensen et al. 2021). This situation is leading to major changes in coastal ecosystems at high latitudes (Krause-Jensen et al. 2021), giving rise to the formation of new habitable areas for primary producers (Hassol 2005). The increase in open water periods suggests a possible expansion and increase in biomass of marine flora on the Arctic coast (Filbee-Dexter et al. 2019; Krause-Jensen et al. 2021). Comparisons between the period 1996/1998 with 2012/2013, in Kongsfjorden, Svalbard, have shown an increase in biomass of some macroalgal species such as *L. digitata* or an increase in depth range *e.g*., *A. esculenta* from 15 to 18 m (Bartsch et al. 2016). Even if an increase in algal biomass occurs in the Arctic, an increase in the loss of diversity of seaweeds and associated organisms is expected, directly affecting the species most sensitive to climate change (Krause-Jensen & Duarte 2014). Also, an increase in the number of seaweed species has been observed in the Kongsfjorden littoral zone (Bischof et al. 2019). On the other hand, some species, such as *S. latissima* or *P. palmata*, were not found inhabiting the shallow water during 2012/2013 in the Kongsfjorden region, due to their pronounced stenohaline features (Fredriksen et al. 2019). However, during this study, the species *P. palmata*, **(Publication I, and II)**, was found inhabiting the Kongsfjorden intertidal.

In the context of climate change, the two seaweeds species studied *D. aculeata* and *P. palmata* can respond physiologically and biochemically to the increase in temperature and its interaction with high irradiance **(Publication I)**. *D. aculeata* as reported in **publication I**, is able to survive under high temperature for a relatively long period of time, while high irradiance affects photosynthetic regulation. Some photosynthetic organisms may be affected by high light intensity, inducing various damages in dark-adapted seaweed (Fredersdorf et al. 2009). In **publication I** it is reported that *D. aculeata* may be strongly affected by increased irradiance in ice-free areas during the Arctic summer. However, some species of Desmarestiales and Laminariales have decreased their depth limit, mainly related to habitat degradation (Kortsch et al. 2012; Bartsch et al. 2016). This habitat degradation is caused by

increased turbidity in the water column due to increased meltwater runoff and low water exchange capacity in fjords and decreasing sea ice (Pavlov et al. 2019; Krause-Jensen et al. 2021).

This statement is consistent with what has been observed for *D. aculeata* in **publication III**, and may explain the presence of a population of this species in the intertidal zone. **Publication III** reveals that, although *D. aculeata* is sensitive to high irradiance, it can regulate the photosynthetic process under daily irradiance cycles as part of the photoacclimation process. On the other hand, the species *P. palmata* and as reported in **publication I**, being a shallow habitat seaweed, is not strongly affected by increasing temperature and high irradiance. The high temperature tolerance of *P. palmata* is consistent with its distribution and with the optimal temperature range described between 6-10 °C (Morgan & Simpson 1981; Laleguerie et al. 2020) in specimens from Canada and the French coasts. Consequently, it is likely that *P. palmata* under the interaction of these factors, may colonise larger areas in the mid-Arctic intertidal, becoming increasingly subjected to the high irradiances and temperatures that occur there.

The interaction of irradiance and low salinity on Arctic seaweeds has been little studied, *e.g D. ramentacea* and *P. palmata* (Karsten et al. 2003). In **publication II**, *P. palmata* in presence of hyposalinity conditions, loses the capacity for daily photosynthetic regulation and some fronds become bleached. Baral (2020) suggests that a low tolerance to hyposalinity conditions in adult seaweeds could have repercussions on the growth of adult individuals, due to the greater energetic effort required to withstand these conditions. In an ecological context, *D. aculeata* in **publication II**, has a high tolerance to low salinity, which does not affect photosynthetic regulation, so it is expected that this alga will be found more commonly at shallower depths in Arctic fjord systems in the future. Finally, some seaweeds will have their geographical distribution and depth limit affected by climate change (Krause-Jensen et al. 2021).

Although *D. aculeata* may not be affected by hyposalinity, the increase in irradiance in the water column due to ice-free zones will limit the distribution of populations that are not adapted to these conditions. *P. palmata*, on the other hand, can and will successfully resist the increase in irradiance and temperature levels, but the hyposalinity conditions due to the melting water will limit the distribution and possible growth of this species in the Arctic region.

8. Concluding remarks and future perspectives

With regard to the hypotheses proposed, it was possible to conclude the following:

Hypothesis I: **The similar geographical distribution of *Desmarestia aculeata* and *Palmaria palmata* will be reflected in similar ecophysiological acclimation mechanisms, under the interaction of drivers such as temperature and irradiance.**

The hypothesis was partially accepted: the similar geographical distribution of *Desmarestia aculeata* and *Palmaria palmata* showed that both species are able to regulate their photosynthetic and biochemical activity depending on the drivers. *D. aculeata* was found to be more sensitive to high irradiance, while *P. palmata* actively acclimated to high temperature and irradiance.

Hypothesis II: **Hyposalinity will affect the photosynthetic and biochemical regulation of the intertidal seaweed *Palmaria palmata*, during daily light cycles simulating the Arctic summer.**

The hypothesis was accepted: simulated hyposalinity conditions affected the response to daily irradiance cycles in *Palmaria palmata*. In the presence of low salinity this seaweed decreased its physiological responsiveness and its biochemical regulation.

Hypothesis III: **Hyposalinity will affect the process of ecophysiological acclimation to high and low irradiance of the Arctic fjord species *Desmarestia aculeata*, reflected in the photosynthetic activity and biochemical content.**

The hypothesis was rejected: hyposalinity conditions do not affect the physiological and biochemical response capacity of the species *Desmarestia aculeata*. This species showed a high capacity to acclimation to the simulated daily irradiance variations.

Climate projections up to the end of the 21st century indicate that temperatures will continue to rise (IPCC 2019); generating an increasing amplitude of change for the different drivers such as, for example, irradiance, UV, salinity, CO_2, pH, nutrients, among others, with presumably increasingly adverse effects on organisms (Bischof et al. 1998; Roleda et al. 2012; Fredersdorf et al. 2009; Diehl et al. 2020; Li et al. 2020; Monteiro et al. 2021). Rising temperatures have been cited as an increasing threat to coastal marine organisms (IPCC 2019; Smale 2020). Temperature is one of the most important abiotic drivers affecting photosynthetic performance of the organisms (Falkowsi & La Roche 1991). On the other hand, irradiance is a central abiotic driver, forming an important part in the regulation of the photosynthetic process (Hurd et al. 2014), and salinity is an abiotic factor, which influences the nutrient uptake capacity and growth rate of seaweeds (Gordillo et al. 2002).

The aim of this study was to provide information on the acclimation process of *D. aculeata* and *P. palmata*, based on the interaction of abiotic factors such as: temperature increase, different irradiance levels and controlled hyposalinity conditions. The results showed how *D. aculeata* and *P. palmata* species, which have a similar geographical distribution, present different acclimation strategies, mainly regulated by the habitat in which they develop, and by the intrinsic physiological-biochemical mechanism of each species **(Publication I)**. **Publication II** revealed that the current presence of hyposalinity conditions in the first layers of the water column affects *P. palmata* populations. The increase in hyposalinity conditions in the Arctic fjords, predicted by the increase in global temperature, is capable of reducing the capacity of *P. palmata* to acclimatise to variations in daily irradiance levels at the physiological and biochemical levels. This may contribute to the reduction or redistribution of *P. palmata* populations in these latitudes, or to a decrease in the growth of individuals of this species.

D. aculeata presented a different acclimation process to that shown by *P. palmata* **(Publication II)**. *D. aculeata* was not affected by the simulated hyposalinity conditions or by the different irradiance levels to which it was subjected. This species showed a high capacity to acclimatise to the interaction of both abiotic factors. These results are strongly related to the population studied, as it inhabits the Kongsfjorden intertidal zone and is acclimatized to stress from abiotic factors. This ecotype, in particular, was noted to exhibit a robust physiological and biochemical response to salinity and daily irradiance interactions. The fact that *D. aculeata* can show different levels of acclimation to high levels of irradiance, and the interaction of irradiance with other abiotic factors **(Publication I, and III)**, shows the need to

broaden the focus and analyse not only the large seaweeds, but also the understorey and intertidal species that are key to the Arctic coastal ecosystem. A deeper understanding of marine biota and their interaction with different factors is and will be key to conserving Arctic marine ecosystems in times of strong change.

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