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Short-term response to light after the polar night in the Arctic kelps *Alaria esculenta* and *Saccharina latissima*

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ABSTRACT

The current absence of ice in early spring in a number of Arctic fjords allows sunlight to penetrate the water column about two months earlier than it used to be when a thick ice cover was present. This can potentially change the growth dynamics of permanent seaweed forests. To elucidate the ability of seaweeds to take advantage of this early available light, growth, photosynthetic performance, and biochemical composition has been analyzed in two major forest-forming algal species, *Alaria esculenta* and *Saccharina latissima*, from Kongsfjorden (Svalbard) collected in early February, and incubated in dim light and dark conditions. For *A. esculenta*, new tissue appeared during the last weeks of the polar night, so that the new and old tissues coexisted in the same individuals and were compared. Dim light triggered positive growth rates. The onset of light led to rapid (1 h) increase in the optimum quantum yield (F_v/F_m) in the new tissue of *A. esculenta*, while the old tissue and *S. latissima* increased their maximum photosynthetic electron transport rate (ETR_m). The new tissue accumulated 3 to 5 times more internal nitrate than the old tissue, but it showed lower content of photosynthetic pigments. Dim light promoted changes in stored carbohydrates in *A. esculenta* while the total C:N:P ratios remained stable in both species. Furthermore, *S. latissima* responded to light by decreasing its $\partial^{13}C$ values, indicating some activation of its carbon concentrating mechanism. Overall, dim light showed the potential to trigger photosynthetic metabolism and growth as early as February.

1. Introduction

Marine seaweeds forests occupy the shallow rocky coastal areas in cold-water regions of the northern hemisphere (Wernberg et al., 2019). These forests are dominated by large brown algae of the order Laminariales (Goldsmit et al., 2021), and to a lesser extent, Desmarestiales (Schimani et al., 2022). In the Arctic, the increase in temperature is being around four times faster than in the rest of the globe (Rantanen et al., 2022). This warming and the concomitant loss of sea ice are predicted to increase the geographic extent and depth range of marine forest vegetation, although the retreat of endemic species has already been reported (Bartsch et al., 2016; Schimani et al., 2022). Observations on the West Spitsbergen Shelf (Svalbard archipelago, Norway) have shown that the dynamic response of the shelf to wind forcing has a profound effect on the heat content of the water. Winter warming is being particularly amplified in Svalbard (Wendisch et al., 2023), so that winter temperature of the West Spitsbergen Shelf has reverted to that typical of fall, interrupting the normal cycle of sea ice formation in the region, leading to ice-free fjord surface all year-round (Cottier et al., 2007; Maturilli et al., 2013). As a consequence, a double situation has evolved that impacts directly on the physiology of the marine forest community. On one side, the increase in temperature, especially during winter, is expected to compromise year to year survival of individuals that rely on previously stored C reserves and low respiration rates (Gordillo et al., 2022). On the other side, the absence of ice allows sunlight to penetrate the water column more than two months earlier than it used to be when a thick ice cover was present until May (Bischof et al., 2002). In the near future, the loss of global glacier mass is predicted to accelerate (Hugonnet et al., 2021), so that the current scenario can be considered to have crossed a point of no return (Kim et al., 2023). Whether the effect of glacial retreat and run-off on marine primary production is positive or negative depends on a multitude of interacting

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factors, but it is expected that light availability will be the major one (Scherrer et al., 2019). An earlier onset of the macroalgal growth season could also change the seasonal nutrient dynamics in the ecosystem.

A photosynthetically active alga can dedicate part of its energy to nutrient uptake and assimilation during the growth period. In Kongsfjorden, annual primary production is limited by nitrate availability which drops from about 10 μM to undetected levels during spring (Van de Poll et al., 2021), leading to a N-limited summer, when sunlight is available 24 h a day. However, seaweed growth can proceed for a few weeks more after N depletion due to nitrate being stored intracellularly during spring. This ability to store nitrate in the vacuole is then a key factor determining the annual growth balance of the macroalgal forests. Arctic macroalgae have been reported to be storage specialist (Korb and Gerard, 2000; Gordillo et al., 2006) with nitrate accumulation factors higher than their cold-temperate counterparts (Gordillo et al., 2002). The measurements of the amount of total N in the tissue and the stored nitrate in the vacuoles at the end of the polar night could constitute a valuable piece of information to understand the annual C and N balance of these organisms, and how they contribute to the ecosystem budget. The onset of light in February is expected to trigger changes in the photosynthetic performance but it is uncertain if these changes would also promote changes in the basic metabolism of C, N and P, including the major biochemical components, namely, carbohydrates, lipids and proteins.

The response of algal physiology to the spring transition from darkness to light has been evaluated under the previous ice-dominant conditions (Bischof et al., 2002; Aguilera et al., 2002); however, those studies were performed later in the year (May–June) and consisted of a rapid transition from darkness to a well illuminated water column with over 12 h of light per day. A new definition of Polar Night based on available light instead of the traditional solar angle definition, sets the end of this period sometime in the second half of January (depending on the full moon contribution), instead of February (Johnsen et al., 2021). In the current situation, the absence of ice-cover involves a dim light environment with short photoperiods (below 12 h of light) starting already between January and February. It remains unclear whether kelps can grow under these conditions, thus anticipating its growing season.

A winter simulation in laboratory conditions has recently revealed that both kelps species analyzed here, *Alaria esculenta* and *Saccharina latissima,* were able to respond rapidly to PAR (Gordillo et al., 2022), but it is still unknown whether this is the case for their populations in their natural environment. In that study, it was found for the first time that *Alaria esculenta* generates new tissue, presumably from the old one, during the last part of the polar night, and in the absence of light, when C fixation most likely does not occur. Thus, thalli showed a marked two-parts anatomy at the moment of light return. The new blade that appeared mostly in the last month of the simulated polar night (16 weeks in total) is regarded as 'new tissue' in this study, while the tissue remaining from the previous year is referred to as 'old tissue'. Once the light is present, the individuals of *A. esculenta* grow from the new tissue while the old tissue is being degraded. In June, in the field, the old tissue is no longer present (personal observation).

The comparison between new and old tissue as defined above has never been tackled, as far as we know (but see Summers et al., 2023). This comparison of photosynthetic performance, photosynthetic pigment content, biochemical composition and nitrate storage ability could help to explain the seasonal dynamics of Arctic kelp forests.

The species studied here, *A. esculenta* and *S. latissima*, along with *Laminaria digitata,* dominate the upper subtidal zone in Kongsfjorden (about the first 10 m depth, Bartsch et al., 2016; Ronowicz et al., 2020), where algal biomass is the highest, particularly since the reduction of ice-scouring.

Saccharina latissima has been previously identified as a species able to thrive under a warmer and more acidic future (higher dissolved CO_2 levels) Arctic better than endemic species such as *Laminaria solidungula* (Iñiguez et al., 2016a), the latter showing a progressive retreat to colder areas in Svalbard (Bartsch et al., 2016). Olischläger et al. (2017) have shown that the Arctic population of *S. latissima* may benefit more from the change in temperature than the same species from cold-temperate areas due to the Arctic ecotype showing a higher sensitivity in terms of photosynthetic and growth performance. On the other hand, *A. esculenta* benefits from higher CO_2 conditions and warmer temperature in comparison with *Desmarestia aculeata*, another forest forming species of the Arctic. Both species can be identified, then, as 'winners' in the new climatic scenario. However, some limitations have also been reported: Gordillo et al. (2022) showed that both species were unable to resume growth after 16 weeks in total darkness at 8 °C, and Bartsch et al. (2016) showed no change in their total biomass present in the fjord in a 2012/2014 survey compared to a 1996/1998.

In the context of the ongoing climate change, it is important to understand the changes occurring in these kelp forests species to elucidate how prone are their ecosystems to be affected. Traditionally, winter sampling has been difficult due to the presence of a thick ice cover at high latitudes. For this reason, winter behavior of the seaweed community has constituted a gap in our knowledge of these systems. The new situation of year-round ice-free fjords represents new opportunities to tackle this gap.

The aim of this study was to elucidate the ability of kelps to respond to dim light using specimens collected *in situ* at the end of the polar night. The photosynthetic efficiency as well as their nitrate storage ability and their biochemical composition have been analyzed for seven days after the onset of light in early February.

2. Materials and methods

2.1. Plant collection and maintenance

Thalli of the kelps *Alaria esculenta* (L.) Greville and *Saccharina latissima* (L.) Lane, Mayes, Druehl & Sanders were collected from Kongsfjorden (Svalbard) at the beginning of February at about 78° 55′ N and 11° 55′ E (old pier) and between 4 and 6 m depth by scuba-diving. Collected individuals were brought to the laboratory in a black plastic bag, selected and placed in the culture tanks the same day. Visually healthy thalli free from epibiota of about 25–30 cm long were cultured in 200 L rectangular fiberglass raceway tanks with running fjord water sand-filtered in a header tank at 1 °C, which was the same as the fjord water temperature. Darkness was ensured by wearing headlamps to work in the culture room equipped with green filters yielding 0.1–0.3 μmol photons m^{-2} s^{-1} at 0.5 m distance from the forehead. Light was measured using a flat sensor (Li-190R, Li-Cor, United States) connected to a Li-Cor-250A radiometer.

2.2. Experimental setup and growth

The day after collection, the experiment started by measuring the initial values of the variables studied (Initial treatment). Algae were left in the raceway tanks at +1 °C for 7 d in darkness and samples were taken for final measurements (Dark treatment). Another set of algae were placed in a separate racetank (same temperature) and supplied with white light by using a daylight fluorescent lamp (OSRAM L 36W/954, Germany) attenuated with a neutral mesh to 6 μmol photons m^{-2} s^{-1} of PAR (400–700 nm wavelength) measured at the surface of the running water in the tank (Light treatment).

The photoperiod was increased daily to match the natural increase starting at 1:23 (L:D) the first day to reach 5.5:18.5 on day 7, when the final measurements were taken, allowing the metabolism to respond to light availability.

Additionally, short-term photosynthetic measurements were taken after 1h light incubation using PAM fluorescence to assess the rapid reaction of the algae to the returning light after months of darkness, without allowing the full metabolism to acclimate to the new situation.

Each sample was taken from the meristematic area of independent individuals, except for the old tissue of *A. esculenta*, for which samples were taken from the middle part of that region of the thallus.

Growth rate was calculated by weighing and tag-labelling 5 thalli of each species and treatment upon collection. Fresh weights were taken on the same day of the experimental setup, and after 7 d in either darkness or dim light (discounting the weight of the plastic label). The relative growth rate (RGR) was calculated as:

$$\mathrm{RGR}\ (\%\ \mathrm{d}^{-1}) = \left[\mathrm{Ln}\left(W_f / W_i\right) \ / \ 7\right] \mathrm{x}\ 100$$

Where W_f is the final fresh weight and W_i is the initial fresh weight.

2.3. Photosynthesis by PAM fluorescence

Chlorophyll fluorescence for photosynthetic performance was measured using a Junior PAM (Walz, Germany) by generating rapid light curves, with actinic light intensities between 22 and 600 μmol photons m^{-2} s^{-1}, measured with a Li-190R flat sensor attached to a Li-250A light meter (Li-Cor, United States). The optimum and effective quantum yields for the charge separation of photosystem II (PS II) reaction centers were measured for samples in the dark and under actinic illumination (F_v/F_m, and $\Delta F/F_m'$, respectively). The electron transport rate (ETR) between PS II and PS I was calculated in short (30 s) incubations for each actinic irradiance as:

$$\mathrm{ETR} = \Delta F/F_m' \times \mathrm{PAR} \times 0.5 \times \mathrm{A}$$

Where $= \Delta F/F_m'$ is the effective quantum yield, 0.5 stands for the assumption of the even contribution of photons to PS II and PS I, PAR is the actinic irradiance (μmol photons m^{-2} s^{-1}), and A is the thallus absorptance.

The thallus absorptance (A) was estimated by placing the thalli between a white LED lamp and the flat light sensor, so that:

$$\mathrm{A} = I_0 - I_t \ / \ I_0$$

Where I_0 is the light irradiance reaching the sensor, and I_t is the irradiance transmitted through the thallus when this is placed covering the sensor, intercepting the light.

From rapid light curves (ETR *vs.* PAR) the following photosynthetic parameters were calculated according to Eilers and Peeters (1988): the maximum electron transport rate (ETR_m); the quantum efficiency for linear electron transport (initial slope, α); and the sub-saturating irradiance (E_k).

2.4. Biochemical composition

Photosynthetic pigment content of chlorophyll *a*, β-carotene, fucoxanthin and violaxanthin were analyzed from freeze-dried material. Pigments were extracted and analyzed by liquid chromatography as previously described (Wulff et al., 2008). In summary, extraction was performed according to Jeffrey and Wright (1997) in 1.5 ml acetone: MeOH (80:20) for 24 h in −20 °C. The extracts were then sonicated for 60 s using a Vibra-cell sonicator equipped with a 3 mm diameter probe and diluted with 100 % MeOH 1:2 or 1:3. HPLC analysis was carried out using an absorbance diode-array detector (Spectraphysics UV6000LP). A C18 Phenomenex Ultracarb 3 μm ODS (20) (150 × 3.2 mm) column and a guard column, SecurityGuard Phenomenex C18 (4 × 3.0 mm), were used. The HPLC system was calibrated with pigment standards from DHI, Water and Environment, Denmark. Peak identities were further confirmed by on-line recording of absorbance spectra (400–700 nm) as described in Jeffrey and Wright (1997).

Total proteins, total lipids, and total carbohydrates were determined from freeze-dried material stored at −80 °C. Total proteins were extracted in phosphate buffer (0.1 M, pH 6.5) with trichloroacetic acid 5 % and incubated for 1 h. The samples were then subsequently washed with 100 % acetone, and SDS (4 %) was used to resuspend the protein extract. Proteins were estimated spectrophotometrically using bicinchoninic acid-copper sulfate for color development and bovine serum albumin as standard and determined spectrophotometrically at 562 nm (Smith et al., 1985).

Total lipids were extracted using a chloroform:methanol (2:1) solution and incubated overnight in darkness (4 °C). The solution was then evaporated with N_2 before acid digestion using sulfuric acid. Lipids were estimated spectrophotometrically using phosphovanillin for color development and cholesterol as standard. Finally, the concentration of lipids was determined also spectrophotometrically at 520 nm (Barnes and Blackstock, 1973).

Total carbohydrates were extracted in hydrochloric acid (5 %) and heated to 80 °C for 2 h. Carbohydrates were estimated using phenol-sulfuric acid for color development and D-glucose as standard, and spectrophotometrically determined at 485 nm (Dubois et al., 1956).

The total C and N content was measured from freeze-dried material using a C:H:N elemental analyzer (Leco CHNS 932, USA).

For internal nitrate concentration, fresh pieces of thalli were rinsed in distilled water, blotted-dried, and immediately frozen at −80 °C and later freeze-dried and stored at −80 °C until analysis. The internal nitrate content (nitrate + nitrite) was estimated by grinding to fine powder the freeze-dried material (3 mg) and adding 5 ml MilliQ water. The extracts were incubated at 30 °C for 30 min, and then centrifuged at 13000 g for 5 min (Gordillo et al., 2006). Nitrate was determined from the supernatant following García-Robledo et al. (2014).

2.5. Stable isotopic discrimination

The abundance of ^{13}C relative to ^{12}C and of ^{15}N relative to ^{14}N in the thalli (2 mg of freeze-dried mass) was determined by mass spectrometry using a DELTA V Advantage (Thermo Electron Corporation, USA) Isotope Ratio Mass Spectrometer (IRMS) connected to a Flash EA 2000 elemental analyzer.

The ^{13}C and ^{15}N isotopic discrimination in the algal samples ($\delta^{13}C$, $\delta^{15}N$) were expressed in the unit notation as deviations from the $^{13}C/^{12}C$ ratio of the Pee-Dee Belemnite $CaCO_3$ (PDB) and from the $^{15}N/^{14}N$ ratio of the atmospheric N_2, respectively:

$$\delta^{13}\mathrm{C}\ (‰) = \left[\left(\frac{C_{13}}{C_{12}}\right)_{sample} \Big/ \left(C_{13}/C_{12}\right)_{PDB}\right] \times 10^3$$

$$\delta^{15}\mathrm{N}\ (‰) = \left[\left(N_{15}/N_{14}\right)_{sample} \Big/ \left(N_{15}/N_{14}\right)_{air}\right] \times 10^3$$

2.6. Statistical analyses and visualisation

All measurements were taken using five independent thalli as replicates in each treatment. When possible, the same thallus was used for the different variables measured. Results are expressed as mean ± standard deviation, and significance of differences set at $P < 0.05$, unless otherwise stated. Data analyses for significant differences and graphs were performed using GraphPad Prism v10.2.1. Differences in growth were tested using *t*-test. Differences for initial values, light and dark treatments were tested using a one-way ANOVA for *Saccharina latissima*. Instead, a two-way ANOVA was used in *Alaria esculenta* to differentiate between the old and the new tissue of the thallus.

3. Results

Most thalli of both *A. esculenta* and *S. latissima* collected from the field showed new tissue being generated recently (according to its aspect, Fig. 1). In the case of *A. esculenta*, all individuals of 20–50 cm in blade length showed a characteristic two-halves morphology, with a new blade being generated in the lower part and an old blade being degraded in the upper part. Small individuals shorter than 20 cm did not show this differentiation, and only new blade was distinguishable (not

Fig. 1. *Alaria esculenta* (a) and *Saccharina latissima* (b) collected from Kongsfjorden in February, at the end of the polar night. Blade length of about 20–30 cm.

shown). In the case of *S. latissima,* new tissue was presumed in the meristematic zone according to the brightness of its surface and its clear color. In many individuals, this recent tissue produced a widening of the blade in that region of the thallus, as shown in Fig. 1. In addition, part of its holdfast also seemed to have been generated recently.

The onset of light stimulated growth in both species. In darkness, the rate of tissue degradation was 0.21 and 0.05 % FW d^{-1} in *A. esculenta* and *S. latissima*, respectively; while the onset of an increasing photoperiod from 1:23 to 5.5:18.5 h (L:D) in a week led to biomass growth rates of 0.35 and 0.08 % FW d^{-1}, respectively (Fig. 2), although data were not significantly different from the rates in the dark for *S. latissima* (Table 1). Data for growth in *A. esculenta* include the whole thallus with no differentiation between the old and the new tissue. If measurements could consider only the new blade it is highly likely that the rates of biomass increase would have been even higher.

The increase in biomass with the onset of light did not trigger an accumulation of photosynthetic pigments. The contents of chlorophyll *a*, β-carotene, fucoxanthin and violaxanthin remained mostly unaltered and were not significantly different from thalli kept in the dark (Table 2). Chlorophyll *a* content differed significantly between the old and the new tissue of *A. esculenta* (Table 1), and similar differences were observed in both β-carotene and violaxanthin, being about half the concentration in the new tissue respect to the old tissue. That was not the case for fucoxanthin, which showed a 50 % higher concentration in the new tissue respect to the old. The antenna size can be estimated from the ratio accessory pigments to chlorophyll *a*. The ratio was significantly higher in the old than in the new tissue in *A. esculenta*, with ratios below 1 (0.36–0.45) indicating small size of antennas, particularly in the new tissue. In *S. latissima*, the ratio was above 1 (1.32 and 1.20 in dark and light, respectively), indicating relatively large antenna size.

Despite the overall constant pigment composition, both species showed changes in their photosynthetic performance. PAM-related parameters were measured as quick responses to light after only 1h of exposure, and then allowing acclimation 7 days later (Fig. 3). The maximum quantum yield for charge separation in photosystem II (F_v/F_m) showed a rapid response in both species, and in the case of *A. esculenta*, also in both types of tissue (old and new). This response was transient in *S. latissima* and the old tissue of *A. esculenta*, going back to the values obtained in the dark of about 0.68. The new tissue of *A. esculenta* had low F_v/F_m values in the dark of about 0.4 that increased

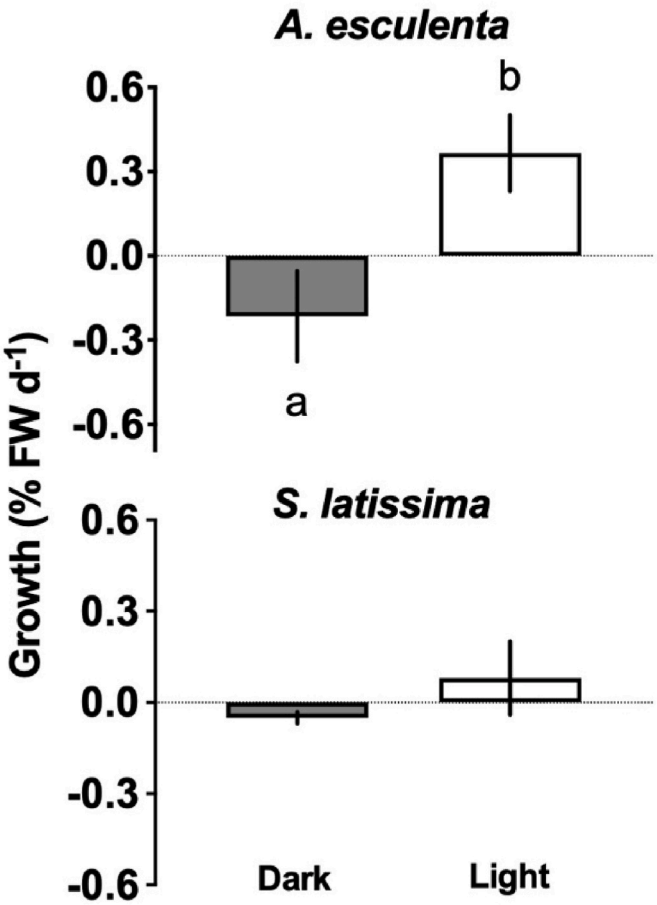

Fig. 2. Growth rates of *Alaria esculenta* and *Saccharina latissima* at the end of the polar night after 7 d in either darkness or dim light with short photoperiod (see text). Different letters for significant differences ($P < 0.05$, $n = 5$).

to 0.5 after 1 h light and matched the old tissue after one week in light (0.67).

Regarding maximum electron transport rate (ETR_m), it did not

Table 1
Statistical parameters obtained from two-way ANOVAs for *Alaria esculenta* and one-way ANOVAs for *Saccharina latissima*. Significant differences ($P < 0.05$) in **bold** (n = 5 unless otherwise indicated). Df, degrees of freedom (numerator, denominator).

Factor	*A. esculenta*									*S. latissima*		
	Light			Tissue			Interaction			Light		
Variable	F	Df	P	F	Df	P	F	Df	P	F	Df	P
Growth[a]	3.36	8	0.01	–	–	–	–	–	–	−1.4	8	0.2
Chlorophyll *a*	4.38	1,16	0.053	10.19	1,16	**0.006**	0.1	1,16	0.756	0.332	1,8	0.749
β-Carotenes	0.44	1,13	0.516	14.83	1,13	**0.002**	0.48	1,13	0.502	2.89	1,7	**0.023**
Fucoxanthin	1.51	1,13	0.24	6.70	1,13	**0.023**	0.2	1,13	0.662	1.03	1,8	0.334
Violaxanthin	2.45	1,13	0.142	5.84	1,13	**0.031**	2.45	1,13	0.142	0.88	1,8	0.404
F_v/F_m	25.1	3,37	**<0.001**	256.4	1,37	**<0.001**	27.7	3,37	**<0.001**	43.1	3,17	**<0.001**
ETR_m	2.25	3,33	0.1**	0.06	3,33	0.808	6.42	3,33	**0.002**	7.05	3,17	**0.02**
α	39.8	3,37	**<0.001**	218.5	1,37	**<0.001**	7.73	3,37	**<0.001**	2.4	3,17	0.104
E_k	7.65	3,33	**<0.001**	43.4	1,33	**<0.001**	16.97	3,33	**<0.001**	10.97	3,17	**0.005**
Total C	0.43	2,24	0.659	35.89	1,24	**<0.001**	4.05	2,24	**0.03**	1.33	2,12	0.301
Total N	1.39	2,24	0.270	0.0	1,24	0.759	2.5	2,24	0.103	1.41	2,12	0.282
C:N	2.89	2,24	0.075	24.17	1,24	**<0.001**	1.45	2,24	0.254	1.39	2,12	0.288
Total P	1.23	2,18	0.316	17.65	1,18	**<0.001**	3.85	2,18	0.041	0.11	2,8	0.893
Internal NO_3^-	2.5	2,20	0.107	105.03	1,20	**<0.001**	1.25	2,20	0.302	18.4	2,11	**<0.001**
Carbohydrates	9.94	2,19	**0.001**	72.93	1,19	**<0.001**	1.45	2,19	0.259	4.87	2,12	**0.028**
Lipids	6.5	2,19	**0.006**	100.78	1,22	**<0.001**	4.32	2,22	**0.026**	1.38	2,12	0.289
Proteins	0.93	2,21	0.412	57.43	1,21	**<0.001**	3.34	2,22	**0.038**	3.11	2,12	0.082
$\delta^{13}C$	10.23	2,24	**<0.001**	11.95	1,24	**0.002**	1.02	2,24	0.376	3.9	2,12	0.05
$\delta^{15}N$	1.47	2,24	0.316	0.034	1,24	0.814	8.09	2,24	**0.005**	5.39	2,12	**0.02**

** Independent analyses applied for both type of tissue (one-way ANOVA) revealed significant differences for the old tissue.
[a] A Student t-test was applied to growth rate.

Table 2
Pigment composition of thalli of *Alaria esculenta* and *Saccharina latissima* at the end of the Polar Night, and after 7 d of light resembling the natural photoperiod. Data are mean ± standard deviation (n = 5). Significant differences for t-tests as an asterisk ($P < 0.05$).

	Dark	Light
Chlorophyll *a* (mg g^{-1} DW)		
A. esculenta new tissue	0.462 ± 0.156	0.326 ± 0.125
A. esculenta old tissue	0.264 ± 0.118	0.163 ± 0.100
S. latissima	0.246 ± 0.135	0.274 ± 0.129
ß-carotene (mg g^{-1} DW)		
A. esculenta new tissue	0.0072 ± 0.0014	0.0072 ± 0.0022
A. esculenta old tissue	0.0044 ± 0.0018	0.0033 ± 0.0013
S. latissima	0.0060 ± 0.0031	0.0107 ± 0.0012*
Fucoxanthin (mg g^{-1} DW)		
A. esculenta new tissue	0.152 ± 0.050	0.133 ± 0.058
A. esculenta old tissue	0.101 ± 0.021	0.061 ± 0.027*
S. latissima	0.293 ± 0.128	0.370 ± 0.106
Violaxanthin (mg g^{-1} DW)		
A. esculenta new tissue	0.0103 ± 0.0053	0.0062 ± 0.0024
A. esculenta old tissue	0.0043 ± 0.0023	0.0043 ± 0.0014
S. latissima	0.0060 ± 0.0031	0.0107 ± 0.0012
Accesories:Chl. *a*		
A. esculenta new tissue	0.36 ± 0.02	0.36 ± 0.03
A. esculenta old tissue	0.45 ± 0.06	0.39 ± 0.03
S. latissima	1.32 ± 0.27	1.20 ± 0.28

increase in the new tissue of *A. esculenta* in light, maintaining values of around 17 μmol $e^- m^{-2} s^{-1}$, while it increased with exposition to light in both the old tissue of *A. esculenta* and in *S. latissima* to 24 and 33 μmol $e^- m^{-2} s^{-1}$, respectively. This increase was particularly strong for the latter, since the initial values were only 5 μmol $e^- m^{-2} s^{-1}$. The response to light involved the photosynthetic efficiency (α) in both types of tissue of *A. esculenta*, but not in *S. latissima*. The strongest increase was recorded in new tissue from 0.07 to 0.21 e^- photons^{-1}, while *S. latissima* showed over 0.2 e^- photons^{-1}already in the dark. As a consequence of changes in both α and ETR_m, the semi-saturation irradiance (E_k) was also affected, so determining the demand of light to saturate photosynthesis. Values of E_k strongly decreased after only 1 h of exposure to light in the new tissue of *A. esculenta* from about 286 to 81 μmol photons $m^{-2} s^{-1}$. However, it showed a significant increase in the old tissue, mostly due to low values in darkness (around 50 μmol photons $m^{-2} s^{-1}$) to similar values to those of the new tissue in light. Similarly, E_k also increased after only 1 h of light in *S. latissima* to values of 65 μmol photons $m^{-2} s^{-1}$, but continued to increase to 138 μmol photons $m^{-2} s^{-1}$ after one week, coming from values as low as 22 μmol photons $m^{-2} s^{-1}$ in the dark.

The total content of both C and N remained fairly constant in both type of tissues of *A. esculenta* and in *S. latissima* despite the light treatment (Tables 1 and 3). Total C values ranged between 21 and 29 % DW, while total N content was between 2.3 and 2.9 % DW. As a consequence, only slight changes were recorded for the C:N ratio, ranging from 12 to 16 mol:mol in *A. esculenta* and from 8.3 to 9.4 in *S. latissima*. Internal P showed significant differences due to light treatment only in the new tissue of *A. esculenta*, pointing to some light-dependent ability to uptake P. The new tissue was in deficit of P respect to the old tissue. Overall, C:N:P ratios departed from the traditional Redfield ratio (106:16:1), ranging about 20–25:2–3:1, which indicates relative low values of both C and N.

The ability to manage internal N reserves was further analyzed measuring the internal nitrate concentration (Fig. 4). In both types of tissue of *A. esculenta*, nitrate was not significantly accumulated nor used up, regardless the light treatment; however, the new tissue accumulated 3 to 5 times more nitrate than the old tissue. In contrast, *S. latissima* seemed to be using its internal nitrate reserves during the last week of the dark period. This net consumption was partially compensated with the presence of light, likely due to the demand of energy to uptake new nitrate from the external medium, although not in significant amount. However, an artifactual effect of culture conditions cannot be ruled out.

The internal biochemical composition of carbohydrates, lipids and proteins showed clear differences between the new and the old tissue of *A. esculenta* (Table 1). The new tissue presented less carbohydrates, less lipids, and particularly less proteins, with its content being 25, 30 and 33 % lower than in the old tissue, respectively (Table 4). The onset of light implied the mobilization of carbohydrates and lipids in both tissues, and also the decrease in protein in the new tissue, but not in the old, probably due to active growth being faster than protein accumulation in the former. In contrast, *S. latissima* showed the highest concentration of carbohydrates in light of about 85 mg g^{-1} DW. Lipid content in *S. latissima* was similar to the new tissue of *A. esculenta* at about 4 mg g^{-1} DW regardless of the light treatment. *S. latissima* showed the lowest protein content, with only about 13 mg g^{-1} DW in any

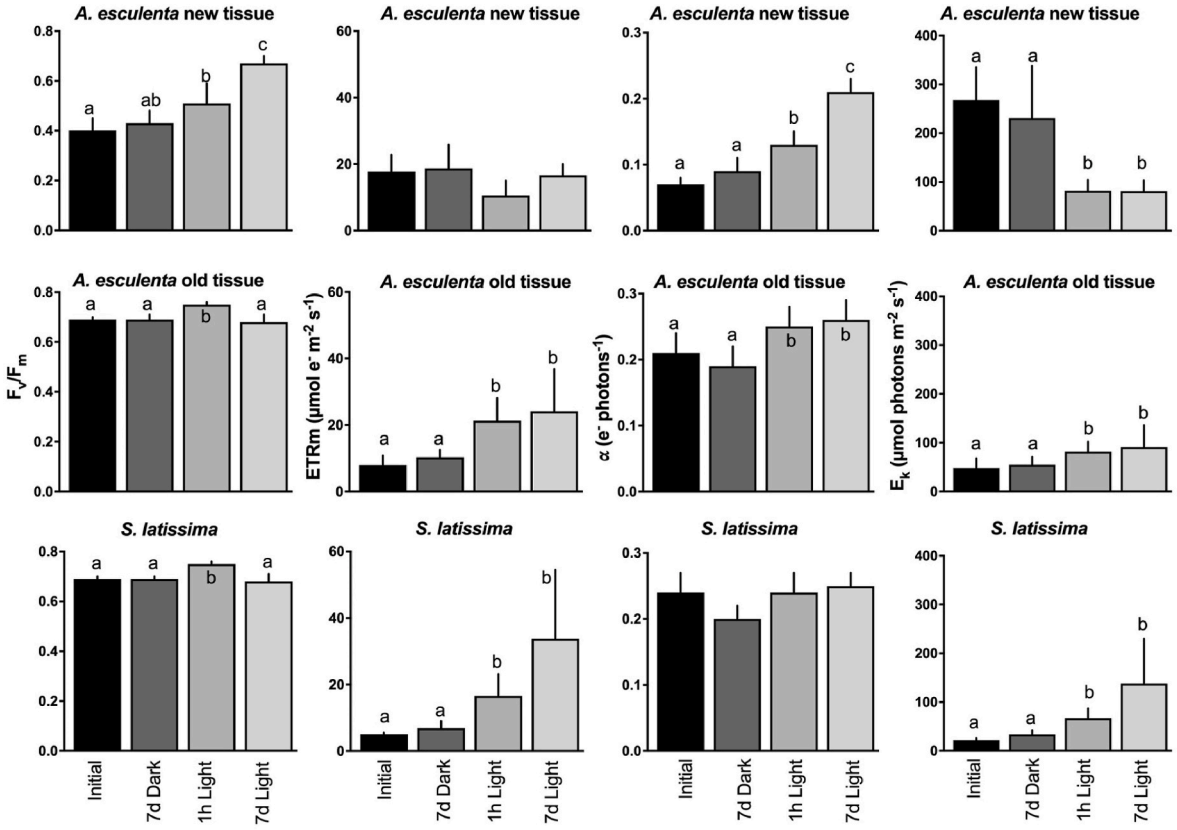

Fig. 3. Optimum quantum yield (F_v/F_m) and parameters derived from rapid light curves (RLCs) measured with PAM fluorescence: Maximum electron transport rate (ETR_m), photosynthetic efficiency (α), and subsaturating PAR (E_k), in thalli of *Alaria esculenta* and *Saccharina latissima* at the end of the Polar Night (initial) and after 7 d of either darkness or light resembling the natural photoperiod. Data are mean ± standard deviation (n = 5). Different letters for significant differences ($P < 0.05$).

Table 3
Total content of carbon, nitrogen, and phosphorus of thalli of *Alaria esculenta* and *Saccharina latissima* at the end of the polar night (initial) and after 7 d of either darkness or light resembling the natural photoperiod. Data are mean ± standard deviation (n = 5). Different letters for significant differences ($P < 0.05$).

	Initial	Dark	Light
Total C (% DW)			
A. esculenta new tissue	25.2 ± 1.4^{a}	24.4 ± 1.7^{a}	23.2 ± 2.1^{a}
A. esculenta old tissue	25.2 ± 1.4^{a}	28.9 ± 2.1^{a}	29.1 ± 1.6^{a}
S. latissima	20.6 ± 2.1^{a}	21.5 ± 3.4^{a}	23.5 ± 3.1^{a}
Total N (% DW)			
A. esculenta new tissue	2.4 ± 0.3^{a}	2.4 ± 0.3^{a}	2.3 ± 0.4^{a}
A. esculenta old tissue	2.4 ± 0.3^{a}	2.4 ± 0.4^{a}	2.6 ± 0.4^{a}
S. latissima	2.9 ± 0.4^{a}	2.6 ± 0.3^{a}	2.9 ± 0.3^{a}
C:N (mol:mol)			
A. esculenta new tissue	12.4 ± 0.8^{a}	11.9 ± 0.8^{a}	12.0 ± 1.3^{a}
A. esculenta old tissue	15.9 ± 1.7^{a}	14.4 ± 1.2^{ab}	13.5 ± 1.6^{b}
S. latissima	8.3 ± 1.5^{a}	9.6 ± 1.3^{a}	9.4 ± 1.0^{a}
Total P (% DW)			
A. esculenta new tissue	1.01 ± 0.13^{a}	0.92 ± 0.19^{a}	0.96 ± 0.19^{a}
A. esculenta old tissue	1.28 ± 0.19^{a}	1.00 ± 0.49^{a}	1.29 ± 0.36^{a}
S. latissima	0.97 ± 0.26^{a}	1.09 ± 0.2^{a}	1.16 ± 0.31^{a}
C:N:P			
A. esculenta new tissue	25 : 2.4:1^{a}	26.5 : 2.6:1^{a}	22.5 : 2.2:1^{a}
A. esculenta old tissue	20 : 1.9 : 1^{a}	29 : 2.4 : 1^{a}	22.5 : 2: 1^{a}
S. latissima	21 : 3: 1^{a}	20 : 2.4 : 1^{a}	20 : 2.5 : 1^{a}

treatment, while the old tissue of *A. esculenta* showed the highest at about 70 mg g^{-1} DW in the dark.

The stable isotopic discrimination values for $\partial^{13}C$ and $\partial^{15}N$ showed fairly constant values, however, some significant differences could be observed (Table 1). In *A. esculenta*, $\partial^{13}C$ was lower in the new than in the old tissue, regardless of the light treatment (Fig. 5). In contrast, *S. latissima* responded to light by decreasing its $\partial^{13}C$ values, indicating some activation of its carbon concentrating mechanism. Values for $\partial^{15}N$ in both *A. esculenta* and *S. latissima* showed no clear pattern, with values around 5–6‰ in both types of tissue, and in both species.

4. Discussion

A fundamental selection pressure imposed on multiyear primary producers at high latitudes is the ability to tolerate long periods of darkness at low temperature. Some polar seaweeds tolerate darkness for up to 18 months (Wiencke, 1990; tom Dieck, 1993). During the dark period, internally programmed circannual changes take place. Summers et al. (2023) have reported that new tissue seemed to have formed during the polar night in *Alaria esculenta* and *Saccharina latissima*, as well as in *Palmaria palmata*, and to a lesser extent, *Laminaria digitata* and *Ulva* sp. from Kongsfjorden. Regarding *A. esculenta*, they only reported longer thalli, thus, probably missing the double blade anatomy observed by us in the laboratory (Gordillo et al., 2022) and in the field (Fig. 2) in February, which indicates that this new blade is formed mostly during the last month of the polar night. The new blade was not observed earlier than in late January–February in our winter simulation study. By June, the old tissue is no longer present in individuals of *A. esculenta* collected from Kongsfjorden (personal observation).

Biomass degradation measured here during the 7 days in darkness at 1 °C was somewhat lower to the average rate observed in lab conditions at 3.5 °C for the whole winter period (Gordillo et al., 2022) in *A. esculenta* (0.21 and 0.71, respectively), and in *S. latissima* (0.05 and 0.35, respectively). In light, growth rates were still far from the maximum rates recorded for these populations of the Kongsfjord. In a recent study (unpublished results), using the same culture setup, we

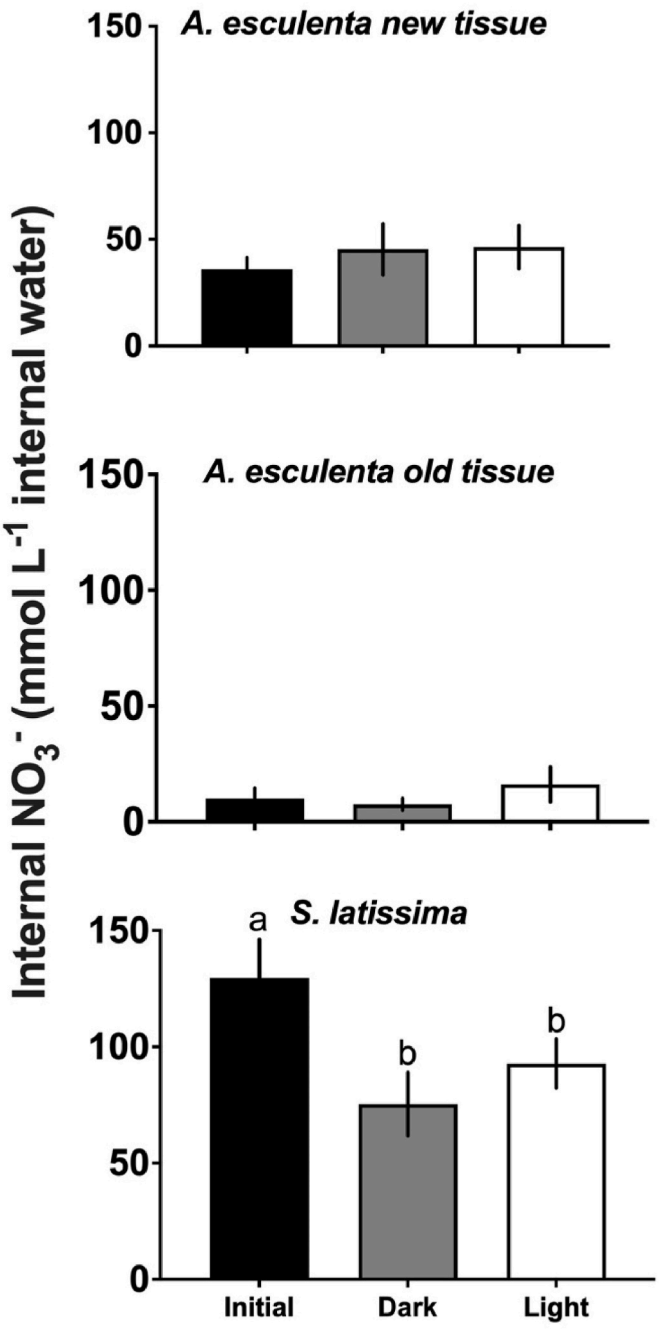

Fig. 4. Internal nitrate concentration in the water of cells of *Alaria esculenta* and *Saccharina latissima* at the end of the polar night (initial) and after 7 d of either darkness or light resembling the natural photoperiod. Data are mean ± standard deviation (n = 5). Different letters for significant differences ($P < 0.05$).

have measured maximum growth rates of 4.4 % FW d^{-1} for *A. esculenta* and 4.0 % FW d^{-1} for *S. latissima*. This means that both species present their optimum growth capacity at the moment in the year that used to coincide with the ice cover breakup. In the present study, they proved to be able to resume growth as soon as light is available, which in an ice-free situation is already in February. According to the AWIPEV COSINA underwater laboratory, PAR can reach over 40 μmol photons m^{-2} s^{-1} at 10 m depth in Kongsfjorden at the beginning of March, well above the compensation point for the photosynthesis for these algae (Gordillo et al., 2022). This anticipation of the macroalgal growth season may trigger consequences in the use of resources such as nutrients,

Table 4
Biochemical composition of soluble carbohydrates, lipids, and soluble protein of the thalli of *Alaria esculenta* and *Saccharina latissima* at the end of the polar night (initial) and after 7 d of either darkness or light resembling the natural photoperiod. Data are mean ± standard deviation (n = 5). Different letters for significant differences ($P < 0.05$).

	Initial	Dark	Light
Soluble carbohydrates (mg glucose equivalent g^{-1} DW)			
A. esculenta new tissue	65.1 ± 6.3[a]	61.8 ± 3.8[a]	52.7 ± 3.9[b]
A. esculenta old tissue	75.8 ± 4.4[a]	74.5 ± 2.6[a]	71.5 ± 1.6[b]
S. latissima	70.5 ± 8.6[a]	71.4 ± 5.1[a]	84.5 ± 10.4[b]
Lipids (mg cholesterol eq. g^{-1} DW)			
A. esculenta new tissue	6.5 ± 1.5[a]	4.6 ± 0.2[b]	3.9 ± 0.7[b]
A. esculenta old tissue	13.4 ± 1.6[a]	14.8 ± 1.8[a]	9.4 ± 3.6[b]
S. latissima	3.6 ± 0.6[a]	3.9 ± 0.9[a]	4.4 ± 0.8[a]
Soluble proteins (mg BSA g^{-1} DW)			
A. esculenta new tissue	22.6 ± 5.4[a]	41.0 ± 7.1[b]	32.1 ± 5.9[b]
A. esculenta old tissue	70.2 ± 12.8[a]	63,2 ± 10.5[a]	58.1 ± 15.6[a]
S. latissima	10.5 ± 1.3[a]	13.6 ± 2.7[a]	12.5 ± 1.6[a]

potentially modifying the annual budget and dynamics of the fjord.

Surviving algae must also be able to resume growth after the dark period, which depends on how active their photosynthetic machinery is. It is a well-known fact that polar algae (both micro- and macroalgae) can sustain an active photosynthetic machinery ready to respond to light availability (e.g. Wulff et al., 2008; Kvernvik et al., 2018; Gordillo et al., 2022; Summers et al., 2023), however, fast reactivation of photosynthesis able to resume growth in natural populations under dim light and short photoperiods has not been proved until now.

In only 1 h of exposure to light, responses are expected to rely on preexisting functional pigment assembly, rather than synthesis *de novo*. In general, the longer the time of light exposure (7 d *vs.* 1 h), the higher the differences in the PAM-related parameters; however, no significant changes in pigment content were recorded. This seems to indicate that light promoted a rearrangement of the preexisting pigment assembly rather than synthesis *de novo* for at least 7 d after the onset of light. A rapid response in PAM-related parameters such as F_v/F_m and ETR_m that is not accompanied by pigment synthesis has also been observed in the Antarctic population of the red *Palmaria decipiens* (Lüder et al., 2002).

Pigment content in our study was similar to that obtained by others for the same species and similar time of the year (Summers et al., 2023); however, these authors failed to identify the new blade, most likely because they measured in January and the new blade seems to generate between January and February (Gordillo et al., 2022). As a consequence, the tissue they identified as 'new' tissue was already formed in the previous October and did not result in differences in pigment content nor in PAM parameters respect to the old tissue. In contrast, the new blade in our study showed marked differences with the old tissue in both pigment content and photosynthetic parameters, although with the same antenna size and ETR_m. The pattern of response to light was different for the new and the old tissues of *A. esculenta* and for *S. latissima*. Rapid (1 h) response promoted an increase in α but not in ETR_m in the new tissue of *A. esculenta* that progressed to day 7. This increase in α was responsible for the decrease observed in E_k, allowing for a better exploitation of low light. In contrast, *S. latissima* was not able to increase its α while it did increase its ETR_m. Consequently, E_k increased. These two different response pattern might be responsible for an earlier onset of growth in *A. esculenta*, while *S. latissima* had to wait for higher PAR intensities sometime later in the year. The old tissue of *A. esculenta* seems to fall in an intermediate position, being able to increase both α and ETR_m but to a lesser extent than the new tissue and *S. latissima*, respectively.

Since the old tissue seems to be unable to survive the spring season, it is still to be determined whether it provides C for the new tissue even during the light. Some indication of this can be derived from the operation of carbon concentrating mechanisms (CCMs). Most algae have developed CCMs that increase the concentration of CO_2 around Rubisco,

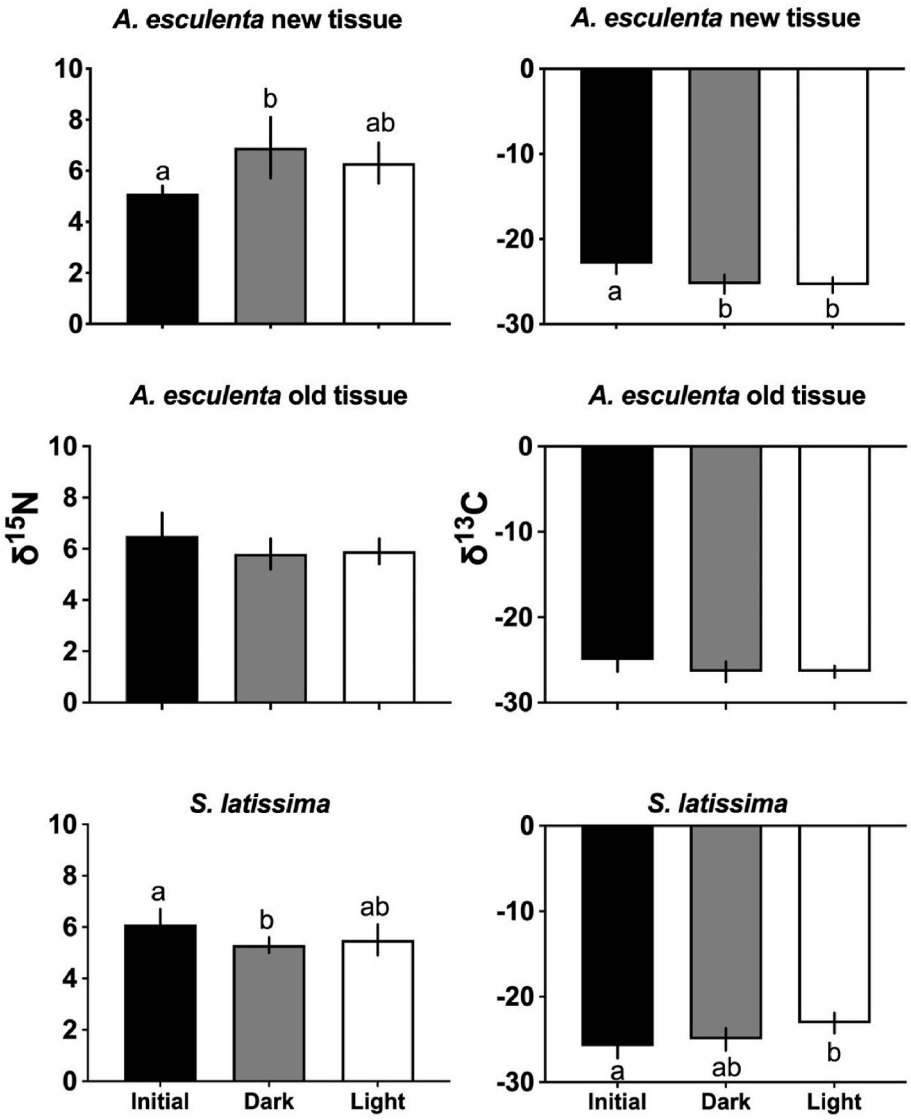

Fig. 5. Stable isotope discrimination of ^{15}N and ^{13}C in thalli of *Alaria esculenta* and *Saccharina latissima* at the end of the polar night (initial) and after 7 d of either darkness or light resembling the natural photoperiod. Data are mean ± standard deviation (n = 5). Different letters for significant differences ($P < 0.05$).

and hence carboxylation. An operating CCM has already been reported in both kelp species studied here (Gordillo et al., 2006), but it is still unknown whether it remains inactive during the polar night and, in that case, if exposure to light reactivates these energy-costly systems. A proxy for CCM activity is the $\partial^{13}C$ value (Velázquez-Ochoa et al., 2022). In general, it is considered as orientative that a $\partial^{13}C$ around or below (less negative) −30 ‰ would indicate inactive CCMs, while values in the −20s ‰ are typical of active CCMs. According to values obtained here, it seems that inorganic C was fixed with the help of CCMs, contributing to the observed growth rates. However, $\partial^{13}C$ does not reflect immediate operation of a CCM, but its activity when C was fixed. At the end of the polar night, we can assume that all organic C comes from C fixation that took place during the previous summer-fall season, not during light-depleted polar night, since CCM requires light energy to operate. Since $\partial^{13}C$ values in the new tissue are similar, even lower, than in the old tissue, it can be hypothesized that C in the new tissue comes from C already fixed in the old tissue in the previous light season and mobilized and rearranged during the last part of the polar night. Scheschonk et al. (2019) described how laminarin was the main organic C compound used as C reserve in winter in *S. latissima*, but it remains to be defined what sort of C molecules are mobilized and transferred to the new blade in *A. esculenta*.

The absence of light precludes the possibility of any net increment of C during the polar night even if nutrients are being uptaken, so that organic C for the new tissue is proposed to be formed from a reconfiguration of the previously formed (old) tissue which implies a mobilization and reallocation of resources internally. This seems to be also the case for nitrate stored intracellularly. Internal levels of nitrate were up to six times higher in the new than in the old tissue, i.e., nitrate in the new tissue will support growth while the old tissue tends to degradation. The internal nitrate levels for *A. esculenta* and *S. latissima* were higher at the end of the polar night than those measured in the same species in June (Gordillo et al., 2006) as expected according to a N-limited summer situation. In agreement with previous knowledge, macroalgae of the Arctic can be considered "storage specialists" (Korb and Gerard, 2000). The onset of light triggered some changes in internal nitrate. In *A. esculenta*, maximum values were recorded in the new tissue in light, but differences were still not significant. *Saccharina latissima*, in contrast, seemed to be using its internal nitrate reserves during the last week of the dark period. This net consumption was partially compensated with light, likely due to the availability of energy to uptake new nitrate from the external medium.

It is generally assumed that darkness survival depends on the C stored during the previous light season (Schenschonk et al., 2019). Since

C reserves are used up during the polar night, C:N:P values reflected this loss of C rather than an uptake of N and P in the absence of light energy. In fact, N:P ratios revealed that N was relatively low to sustain growth. In contrast, known C:N values for summer were clearly higher, reflecting both C accumulation and N limitation (Gordillo et al., 2006).

The impairment of C and N acquisition could lead to different biomass composition. For instance, *S. latissima* showed the highest concentration of carbohydrates in light, along with restricted growth, showing that photosynthetic C was accumulated and could not be used for new biomass production, probably due to insufficient N. That was not the case for *A. esculenta*, where no carbohydrates accumulated and growth could start in light, probably due to an accompanying N uptake being resumed. Major differences were found between the old and the new tissue of *A. esculenta*. The lower concentration of all major components agrees with a new tissue displaying fast growth. The higher concentration in protein in the old tissue respect to the new one explains that total N is similar in both tissues. In the old one N is mainly in the form of protein, while in the new one is in the form of stored nitrate ready to be used for protein synthesis during growth, especially once light is available for the completion of nitrate assimilation. Nevertheless, 7 d of dim light and short photoperiod does not seem enough to observe protein accumulation.

As concluding remarks, the absence of ice cover allows for the onset of macroalgal growth two months earlier than it used to be when ice was present until May. Macroalgae can respond rapidly to the availability of light even during the short photoperiods of February–March due to their photosynthetic machinery being preserved during the polar night. In the case of *A. esculenta*, the new blade tissue that appears at the end of the polar night has the ability to concentrate nitrate and fucoxanthin as well as other resources, presumably being mobilized and reallocated from the old tissue, that are responsible for the active growth even in low light. In contrast, *S. latissima* resume photosynthesis rapidly but does not resume growth as fast as *A. esculenta*, probably due to insufficient energy allocated to N uptake and assimilation.

CRediT authorship contribution statement

Pablo Cobos: Writing – original draft, Formal analysis, Data curation. **Francisco JL. Gordillo:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Patricia Roza:** Formal analysis, Data curation. **Angela Wulff:** Supervision, Resources, Methodology, Formal analysis, Data curation. **Carlos Smerdou:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Ethical approval

Our work requires no ethics approval, since no work on animals was conducted.

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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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Data availability

Data will be made available on request.

References

Aguilera, J., Bischof, K., Karsten, U., Hanelt, D., Wiencke, C., 2002. Seasonal variation in ecophysiological patterns in macroalgae from an Arctic fjord. II. Pigment accumulation and biochemical defence systems against high light stress. Mar. Biol. 140 (6), 1087–1095. https://doi.org/10.1007/s00227-002-0792-y.

Barnes, H., Blackstock, J., 1973. Estimation of lipids in marine animals and tissues: detailed investigation of the sulphophosphovanilun method for 'total' lipids. J. Exp. Mar. Biol. Ecol. 12, 103–118. https://doi.org/10.1016/0022-0981(73)90040-3.

Bartsch, I., Paar, M., Fredriksen, S., Schwanitz, M., Daniel, C., Hop, H., Wiencke, C., 2016. Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming. Polar Biol. 39 (11), 2021–2036. https://doi.org/10.1007/s00300-015-1870-1.

Bischof, K., Hanelt, D., Aguilera, J., Karsten, U., Vögele, B., Sawall, T., Wiencke, C., 2002. Seasonal variation in ecophysiological patterns in macroalgae from an Arctic fjord. I. Sensitivity of photosynthesis to ultraviolet radiation. Mar. Biol. 140 (6), 1097–1106. https://doi.org/10.1007/s00227-002-0795-8.

Cottier, F.R., Nilsen, F., Inall, M.E., Gerland, S., Tverberg, V., Svendsen, H., 2007. Wintertime warming of an Arctic shelf in response to large- scale atmospheric circulation. Geophys. Res. Lett. 34, 10607. https://doi.org/10.1029/2007GL029948.

Dubois, M., Gilles, K.A., Hamilton, J.K., Rebers, P.A., Smith, F., 1956. Colorimetric Method for Determination of Sugars and Related Substances. University of Minnesota. https://edisciplinas.usp.br/pluginfile.php/5012807/mod_resource/content/0/Dubois_1956%20%28m%C3%A9todo%29.PDF.

Eilers, P., Peeters, J.C.H., 1988. A model for the relationship between light intensity and the rate of photosynthesis in phytoplankton. Ecol. Model. 42, 99–215. https://doi.org/10.1016/0304-3800(88)90057-9.

García-Robledo, E., Corzo, A., Papaspyrou, S., 2014. A fast and direct spectrophotometric method for the sequential determination of nitrate and nitrite at low concentrations in small volumes. Mar. Chem. 162, 30–36. https://doi.org/10.1016/j.marchem.2014.03.002.

Goldsmit, J., Schlegel, R.W., Filbee-Dexter, K., MacGregor, K.A., Johnson, L.E., Mundy, C.J., Savoie, A.M., McKindsey, C.W., Howland, K.L., Archambault, P., 2021. Kelp in the Eastern Canadian arctic: current and future predictions of habitat suitability and cover. Front. Mar. Sci. 18. https://doi.org/10.3389/fmars.2021.742209.

Gordillo, F.J.L., Aguilera, J., Jiménez, C., 2006. The response of nutrient assimilation and biochemical composition of Arctic seaweeds to a nutrient input in summer. J. Exp. Bot. 57 (11), 2661–2671. https://doi.org/10.1093/jxb/erl029.

Gordillo, F.J.L., Carmona, R., Jiménez, C., 2022. A warmer arctic compromises Winter survival of habitat-forming seaweeds. Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.750209.

Gordillo, F., Dring, M., Savidge, G., 2002. Nitrate and phosphate uptake characteristics of three species of brown algae cultured at low salinity. Marine Ecology Progress Series 234, 111–118. https://doi.org/10.3354/meps234111.

Hugonnet, R., McNabb, R., Berthier, E., et al., 2021. Accelerated global glacier mass loss in the early twenty-first century. Nature 592, 726–731. https://doi.org/10.1038/s41586-021-03436-z.

Iñiguez, C., Carmona, R., Lorenzo, M.R., Niell, F.X., Wiencke, C., Gordillo, F.J.L., 2016. Increased temperature, rather than elevated CO_2, modulates the carbon assimilation of the Arctic kelps *Saccharina latissima* and *Laminaria solidungula*. Mar. Biol. 163 (12), 248. https://doi.org/10.1007/s00227-016-3024-6.

Jeffrey, S.W., Wright, S.W., 1997. Qualitative and quantitative HPLC analysis of SCOR reference culture collections. In: Jeffrey, S.W., Mantoura, R.F.C., Wright, S.W. (Eds.), Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods. UNESCO Publ, Paris, pp. 343–360.

Johnsen, G., Zolich, A., Grant, S., Bjørgum, R., Cohen, J.H., McKee, D., Kopec, T.P., Vogedes, D., Berge, J., 2021. All-sky camera system providing high temporal resolution annual time series of irradiance in the Arctic. Appl. Opt. 60, 6456–6468. https://doi.org/10.1364/AO.424871.

Kim, Y.H., Min, S.K., Gillett, N.P., Notz, D., Malinina, E., 2023. Observationally-constrained projections of an ice-free Arctic even under a low emission scenario. Nat. Commun. 14 (1). https://doi.org/10.1038/s41467-023-38511-8.

Korb, R., Gerard, V., 2000. Nitrogen assimilation characteristics of polar seaweeds from differing nutrient environments. Mar. Ecol. Prog. Ser. 198, 83–92. https://doi.org/10.3354/meps198083.

Kvernvik, A.C., Hoppe, C.J.M., Lawrenz, E., Prášil, O., Greenacre, M., Wiktor, J.M., Leu, E., 2018. Fast reactivation of photosynthesis in arctic phytoplankton during the polar night. J. Phycol. 54 (4), 461–470. https://doi.org/10.1111/jpy.12750.

Lüder, U.H., Wiencke, C., Knoetzel, J., 2002. Acclimation of photosynthesis and pigments during and after six months of darkness in *Palmaria decipiens* (rhodophyta): a study

to simulate antarctic winter sea ice cover. J. Phycol. 38 (5), 904–913. https://doi.org/10.1046/j.1529-8817.2002.t01-1-01071.x.

Maturilli, M., Herber, A., König-Langlo, G., 2013. Climatology and time series of surface meteorology in Ny-Ålesund, Svalbard. Earth Syst. Sci. Data 5, 155–163. https://doi.org/10.5194/essd-5-155-2013, 2013.

Olischläger, M., Iñiguez, C., Koch, K., Wiencke, C., Gordillo, F.J.L., 2017. Increased pCO_2 and temperature reveal ecotypic differences in growth and photosynthetic performance of temperate and Arctic populations of *Saccharina latissima*. Planta 245 (1), 119–136. https://doi.org/10.1007/s00425-016-2594-3.

Rantanen, M., Karpechko, A. Yu, Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., Laaksonen, A., 2022. The Arctic has warmed nearly four times faster than the globe since 1979. Commun. Earth Environ. 3 (1), 168. https://doi.org/10.1038/s43247-022-00498-3.

Ronowicz, M., Włodarska-Kowalczuk, M., Kukliński, P., 2020. Glacial and depth influence on sublittoral macroalgal standing stock in a high-Arctic fjord. Cont. Shelf Res. 194. https://doi.org/10.1016/j.csr.2019.104045.

Scherrer, K.J.N., Kortsch, S., Varpe, ø., Weyhenmeyer, G.A., Gulliksen, B., Primicerio, R., 2019. Mechanistic model identifies increasing light availability due to sea ice reductions as cause for increasing macroalgae cover in the Arctic. Limnol. Oceanogr. 64 (1), 330–341. https://doi.org/10.1002/lno.11043.

Scheschonk, L., Becker, S., Heheman, J.H., Diehl, N., Karsten, U., 2019. Arctic kelp eco-physiology during the polar night in the face of global warming: a crucial role for laminarin. Mar. Ecol. Prog. Ser. 611, 59–74. https://doi.org/10.3354/meps12860.

Schimani, K., Zacher, K., Jerosch, K., Pehlke, H., Wiencke, C., Bartsch, I., 2022. Video survey of deep benthic macroalgae and macroalgal detritus along a glacial Arctic fjord: kongsfjorden (Spitsbergen). Polar Biol. 45 (7), 1291–1305. https://doi.org/10.1007/s00300-022-03072-x.

Smith, P.K., Krohn, R.I., Hermanson, G.T., Mallia, A.K., Gartner, F.H., Provenzano, M.D., Fujimoto, E.K., Goeke, N.M., Olson, B.J., Klenk, D.C., 1985. Measurement of protein using bicinchoninic acid. Anal. Biochem. 150, 76–85. https://doi.org/10.1016/0003-2697(85)90442-7.

Summers, N., Fragoso, G.M., Johnsen, G., 2023. Photophysiologically active green, red, and brown macroalgae living in the Arctic Polar Night. Sci. Rep. 13 (1). https://doi.org/10.1038/s41598-023-44026-5.

Tom Dieck, I., 1993. Temperature tolerance and survival in darkness of kelp gametophytes (Laminariales, Phaeophyta): ecological and biogeographical implications. Mar. Ecol. Prog. Ser. 100, 253–264.

Van de Poll, W.H., Maat, D.S., Fischer, P., Visser, R.J.W., Brussaard, C.P.D., Buma, A.G.J., 2021. Solar radiation and solar radiation driven cycles in warming and freshwater discharge control seasonal and inter-annual phytoplankton chlorophyll *a* and taxonomic composition in a high Arctic fjord (Kongsfjorden, Spitsbergen). Limnol. Oceanogr. 66 (4), 1221–1236. https://doi.org/10.1002/lno.11677.

Velázquez-Ochoa, R., Ochoa-Izaguirre, M.J., Soto-Jiménez, M.F., 2022. An analysis of the variability in $\delta^{13}C$ in macroalgae from the Gulf of California: indicative of carbon concentration mechanisms and isotope discrimination during carbon assimilation. Biogeosciences 19, 1–27. https://doi.org/10.5194/bg-19-1-2022.

Wendisch, M., et al., 2023. Atmospheric and surface processes, and feedback mechanisms determining arctic amplification: a review of first results and prospects of the (AC)3 Project. Bull. Am. Meteorol. Soc. 104, E208–E242. https://doi.org/10.1175/BAMS-D-21-0218.1.

Wernberg, T., Krumhansl, K., Filbee-Dexter, K., Pedersen, M.F., 2019. Status and trends for the world's kelp forests. In: Sheppard, C. (Ed.), World Seas: an Environmental Evaluation, second ed. Academic Press, United Kingdom, pp. 57–78. https://doi.org/10.1016/B978-0-12-805052-1.00003-6.

Wiencke, C., 1990. Seasonality of brown macroalgae from Antarctica—a long-term culture study under fluctuating Antarctic daylengths. Polar Biology 10, 589–600.

Wulff, A., Roleda, M.Y., Zacher, K., Wiencke, C., 2008. Exposure to sudden light burst after prolonged darkness—a case study on benthic diatoms in Antarctica. Diatom Res. 23 (2), 519–532. https://doi.org/10.1080/0269249X.2008.9705774.