



Impacts of combined temperature and salinity stress on the endemic Arctic brown seaweed *Laminaria solidungula* J. Agardh

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Abstract

Macroalgae such as kelp are important ecosystem engineers in the Polar Regions and potentially affected by freshening and ocean warming. The endemic Arctic kelp *Laminaria solidungula* might be particularly imperiled and become locally extinct from Arctic fjord systems in the future, since temperature increase is most pronounced in the Polar Regions. Additionally, increased temperatures cause glacier and sea ice melting and enhancing terrestrial run-off from snowfields, which eventually can result in hyposaline conditions in fjord systems. We conducted a multiple-stressor experiment at four temperatures (0, 5, 10, 15 °C) and two salinities (S_A 25, 35) to investigate the combined effects of increasing temperature and decreasing salinities on the physiological and biochemical status of young *L. solidungula* sporophytes. Both drivers had significant and interacting impacts, either in an additive or antagonistic way, dependent on the respective response variable. The maximum quantum yield of photosystem II (F_v/F_m) significantly declined with temperature increase and low salinity. Even though the absolute pigment content was not affected, the deepoxydation state of the xanthophyll cycle increased with intensified stress. Higher temperatures affected the C:N ratio significantly, mainly due to reduced nitrogen uptake, while S_A 25 supported the nitrogen uptake, resulting in an attenuation of the effect. The concentration of mannitol decreased at S_A 25. At control S_A 35 mannitol level remained steady between 0 and 10 °C but significantly decreased at 15 °C. Conclusively, our results show that *L. solidungula* is very susceptible to both drivers of climate change, especially when they are combined. Implications to species ecology are discussed.

Keywords Kelp · Multiple-stressor · Mannitol · F_v/F_m · C:N · DPS

Introduction

Temperature increase is one of the major drivers of climate change. The strongest regional warming over the last 30 years was detected in the Polar Regions (Maturilli et al. 2013; Meredith et al. 2019). Elevated air and sea water temperatures cause glacier and sea ice melting and increased terrestrial run-off from snowfields (Sundfjord et al. 2017;

Filbee-Dexter et al. 2019). Consequently, increased temperatures may result in hyposaline conditions in Arctic fjords, due to limited seawater exchange and stratification (Svendsen et al. 2002). Between 1936 and 1999 total fresh water inflow into the Arctic Ocean increased by about 7% (Bluhm and Gradinger 2008). Under regular conditions, seawater salinity in Arctic fjords averages S_A 34.5 in spring, and can drop below S_A 23 at the sea surface (Karsten et al. 2003; Zacher et al. 2009). However, salinity in deeper water layers down to 20 m may also be affected after vertical mixing by wave and wind action (Hanelt et al. 2001). Average seawater temperatures in Kongsfjorden, Svalbard are 4 °C during summer, but can reach a maximum of 5–7 °C (Hanelt et al. 2001; Svendsen et al. 2002; Bartsch et al. 2016). In 2019, these maxima were exceeded reaching almost 8 °C, which demonstrates the regional fast increases of seawater temperature (unpublished; Dashboard AWI 2019). In other Arctic regions, the sea surface temperature has already increased up to 8–10 °C (Wiencke et al. 2007). Long-term trends for

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the Arctic region predict a further increase in warming and reduction of sea ice cover (Müller et al. 2009; Walczowski et al. 2012; Oliver et al. 2018), and increasing temperatures, especially heat wave events, are likely to impact many marine species (Smale et al. 2019).

Arctic macroalgae are specifically affected by freshening and ocean warming (Hanelt et al. 2001). More than 140 seaweed species in the Arctic region have been described so far, most of them growing in the sublittoral (Hop et al. 2012). Kelps, large brown seaweeds of the order Laminariales, are important ecosystem engineers in Arctic fjords. The only endemic kelp species from the Arctic is *Laminaria solidungula* J. Agardh, which can be found down to depths of 18 m (Roleda 2016). It grows at temperatures up to 16 °C with an optimum at 5–10 °C (tom Dieck (Bartsch) 1992). Despite the general ability of seaweeds to acclimate to variation in temperature and other environmental drivers (e.g., Davison et al. 1991; Bischof et al. 2002; Graiff et al. 2015b; Diehl et al. 2019), there is growing concern that *L. solidungula* might become locally extinct from Arctic fjord systems in the future (Müller et al. 2009). Temperature stress can result in structural weakening of kelp tissue (Simonson et al. 2015b) and has an influence on carbon and nitrogen content, due to structure and nitrogen storage (Atkinson and Smith 1983; Peters et al. 2005). It also affects photosynthetic quantum yield (F_v/F_m) and pigment concentrations (Andersen et al. 2013; Fernandes et al. 2016). Various, potentially interacting, drivers may additionally influence kelp fitness and competitive success. In order to cope with variation in environmental drivers, such as salinity or irradiation, seaweeds developed different acclimation mechanisms to maintain cellular functions (e.g., Karsten and West 2000; Eggert et al. 2007; Rautenberger et al. 2015; Ji et al. 2016). Among others, brown algae synthesize the polyol mannitol to compensate osmotic stress (Iwamoto and Shiraiwa 2005). Mannitol acts as a compatible solute, by conserving intracellular homeostasis and potentially functioning as antioxidant (Kirst 1989; Iwamoto and Shiraiwa 2005; Eggert et al. 2007). Furthermore, it is known that salinity changes substantially affect nitrogen metabolism in seaweed (Gordillo et al. 2002; Mandal et al. 2015).

Consequently, kelp forests have already been directly and indirectly impaired by large-scale environmental change (Müller et al. 2009; Bartsch et al. 2016). Until today most studies on environmental impacts on seaweeds were designed as uni-factorial experiments (e.g., Bischof 2002; Karsten 2007; Wiencke et al. 2007; Olischläger et al. 2012; Simonson et al. 2015a) or studied interactions between irradiation or acidification and temperature (e.g., Fredersdorf et al. 2009; Heinrich et al. 2015; Gordillo et al. 2016; Springer et al. 2017).

While the effects of irradiance and temperature on kelps have been studied in detail, little is known on salinity

tolerance of polar seaweeds (e.g., Karsten et al. 1991a, b; Jacob et al. 1991; 1992; Karsten 2007; Li et al. 2019), and even less on salinity temperature interactions (Russell 1987; Thomas et al. 1988; Fredersdorf et al. 2009; Mandal et al. 2015), especially with regard to the endemic kelp *L. solidungula*.

The present study reveals physiological and biochemical responses to increasing temperature and changing salinities for the hitherto understudied Arctic endemic kelp species *Laminaria solidungula*. Results obtained shed light on the adaptive responses of the species to predict kelp performance in a continuously changing Arctic environment.

Material and methods

Laminaria solidungula cultivation

A gametophyte strain of *Laminaria solidungula* (as stock culture obtained from the Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany; AWI culture number 3130—not separated into male and female gametophytes) from Spitsbergen was fragmented into multicellular gametophyte filaments and subjected to 0 °C, short-day conditions (4:20-h-light:dark [LD]) for induction of fertility (tom Dieck 1989). After a month, fragments were transferred into long-day conditions (16:8-h-LD). The first sporophytes became visible after 2 months, and were transferred into larger aerated glassware during growth. The size of the glassware was adapted to the size of sporophytes. After 5 months, the sporophytes were transferred to 5 °C 16:8-h-LD conditions to promote further growth. The sporophytes were cultivated at a photon fluence rate of 30 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (ProfiLux 3 with LED Mitras daylight 150, GHL Advanced Technology, Kaiserslautern, Germany). The sporophytes were initially cultivated with full Provasoli-enriched seawater (PES; sterile sea water from the North Sea) and after another 5 months onwards in 1/2 PES (with Hepes buffer, respectively). The medium was changed every 1–2 weeks. One month later, the sporophytes were once again transferred into 0 °C to delay growth until the experiment was conducted 6 weeks later.

Two-factorial stress experiment: temperature and salinity

Young sporophytes of *Laminaria solidungula* were maintained in aerated 2-L Kautex bottles filled with 1/2 PES at an artificial photon fluence rate of 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and a 16:8-h-LD (ProfiLux 3 with LED Mitras daylight 150, GHL Advanced Technology, Kaiserslautern, Germany). The medium was changed twice a week. The samples were acclimated to four different temperatures (0, 5, 10, 15 °C)

within 1 week. The salinity treatments (S_A 25 and 35) were started after temperature acclimation. The hyposaline conditions were maintained by diluting the sterile sea water (North Sea) with freshwater (tap water). The treatment 0 °C, S_A 35 was used as control. Four sporophytes were cultivated as replicates ($n = 4$) per treatment. After being maintained at treatment conditions for 14 days, all samples were shock frozen in liquid N_2 , stored at -80 °C, and freeze-dried before biochemical analyses.

Response variables

Photo-ecophysiological markers

The photosynthetic performance of the meristem was determined every fourth day by measuring the *in vivo* chlorophyll-fluorescence of photosystem II (PSII) using an Imaging-PAM (Walz GmbH Mess- und Regeltechnik, Effeltrich, Germany), after 5 min of dark acclimation. The PAM was set up to determine the amplitude of the fluorescence signal (F_v) between 0.15 and 0.2 as recommended in the manual (IMAGING-PAM M-Series Chlorophyll Fluorometer, Heinz Walz GmbH, Effeltrich, Germany). The maximum quantum yield of photosystem II (F_v/F_m) represents a sensitive indicator of photosynthetic performance and, hence, of algal fitness, which might be affected by stress exposure (Kirst 1989; Nitschke et al. 2014; Ji et al. 2016).

Photosynthetic and accessory pigments ($n = 4$) were extracted and analyzed following exactly Koch et al. (2015). Therefore, 0.05–0.1 g freshly freeze-dried samples were extracted in 1 mL Acetone (90%, v/v), incubated at 4 °C for 24 h in darkness and analyzed with a High-Performance Liquid Chromatography (HPLC). The concentrations of chlorophyll *a* and *c2* (Chl *a*, Chl *c2*), fucoxanthin (Fuc), β -carotene (β -Car) as well as the pool-size of the xanthophyll cycle (VAZ = violaxanthin, antheraxanthin, zeaxanthin) were calculated as $\mu\text{g g}^{-1}$ dry weight (DW). The deepoxydation state (DPS) of the xanthophyll cycle was calculated after Colombo-Pallotta et al. (2006).

Additionally, the antioxidant phlorotannin was determined after Springer et al. (2017) using the Folin–Ciocalteu method described in Cruces et al. (2012). 20 mg of freeze-dried sample ($n = 4$) was extracted in 1 mL Acetone (70% v/v) and incubated for 24 h at 4 °C in darkness. For the analyses, the absorption at λ 730 nm of three aliquots per replicate was determined in a microplate photometer. The total soluble phlorotannin concentration was expressed in mg g^{-1} DW.

Mannitol

1 mL aqueous Ethanol (70%, v/v) was added to three aliquots of 15–20 mg of each lyophilized and homogenized sample

and incubated in a water bath at 70 °C for 3–4 h ($n = 4$). The vials were vortexed occasionally to keep the samples dispersed. Initially, samples were centrifuged (5 min; 13,000 rpm) and 800 μL of the supernatant was transferred to a fresh vial and evaporated to dryness (Alpha 1–4 LSC-plus and RVC 2–25 CDplus, Martin Christ Gefriertrocknungsanlagen GmbH, Osterode am Harz, Germany). The pellets were re-dissolved by vortexing and ultrasonic treatments in 800 μL HPLC grade water. The samples were then centrifuged for another 5 min (13,000 rpm). The obtained supernatant was analyzed using the method of Karsten et al. (1991a) in a HPLC Agilent Technologies system (1200 Series, Santa Clara, California, USA) with an Aminex Fast Carbohydrate Analysis Column HPAP (100 \times 7.8-mm, 9- μm , BioRad, Munich, Germany), protected by a guard cartridge (Phenomenex, Carbo-Pb-2 + 4 \times 3.00-mm I.D., Aschaffenburg, Germany) with 100% dH_2O as a mobile phase. The flow rate was adjusted to 1 mL min^{-1} at 10–100 bar and 70 °C. For the calibration 0.5, 1.0, 2.5, 5.0 and 10.0 mM D(-)-mannitol standards ($\text{C}_6\text{H}_{14}\text{O}_6$, Roth) were used. Absorption peaks were detected via RI-Detector (35 °C) and analyzed using the software ‘ChemStation for LC 3D systems’ (Agilent Technologies, Waldbronn, Germany). Mannitol contents were calculated in $\mu\text{mol g}^{-1}$ dry weight (DW).

Carbon, nitrogen and C:N ratio

Total carbon (C) and total nitrogen (N) concentrations as well as C:N ratios were analyzed following Graiff et al. (2015a). Three aliquots of 2 mg ($n = 4$) of lyophilized and ground samples were weighed into tin cartridges (6 \times 6 \times 12-mm) and combusted at 950 °C. Acetanilide ($\text{C}_8\text{H}_9\text{NO}$) was used as standard (Verardo et al. 1990). The contents of C and N were quantified automatically in an elemental analyzer (Vario EL III, Elementar, Langensfeld, Germany). Total C and total N contents were expressed in mg g^{-1} dry weight (DW).

Statistical analysis

All datasets were tested for normal distribution (Shapiro–Wilk test; $p > 0.05$) and for homogeneity (Levene’s test; $p > 0.05$). Data were transformed if needed. Afterwards, two-way ANOVAs were performed for each parameter ($p < 0.05$) and a post hoc Tukey’s test applied to reveal significant differences ($p < 0.05$). The pigment datasets were analyzed using the generalized linear model (GLM) ($p < 0.05$). The statistical analyses were run using RStudio (Version 1.1.383, Boston, MA, USA) and Excel 2016 (Windows; Microsoft Corporation, Redmond, WA, USA).

Results

Photo-ecophysiology

After 14 days, photosynthetic maximum quantum yield (F_v/F_m) showed a significant decrease at 15 °C in both salinities and was significantly lower than the control treatment ($F_3 = 62.866$, $p < 0.0001$). In all other treatments, the maximum values of 0.684 ± 0.012 ($n = 4$) were maintained, independent of temperature or salinity. After 7 days of temperature acclimation, F_v/F_m differed between the four temperatures (0.595 ± 0.015 – 0.678 ± 0.010 ; control: 0.616 ± 0.017 ; $n = 4$) but did not significantly change with temperature and salinity stress during the first 11 days

of the experiment (Fig. 1). The low salinity treatment at 15 °C impaired F_v/F_m significantly stronger than the control salinity treatment (S_A 25: 0.396 ± 0.128 ; S_A 35: 0.533 ± 0.034 ; $n = 4$; $p = 0.0001$) (Fig. 1).

Pigment concentrations (GLM: $p < 0.05$, details: Supplementary Table 1) and phlorotannin concentrations (temperature: $F_3 = 11.115$, $p < 0.0001$; salinity: $F_1 = 5.884$, $p = 0.0232$; interaction: $F_3 = 3.078$, $p = 0.0467$) exhibited few significant differences, which, however, could not be assigned to any of the stress treatments (Table 1). Nevertheless, the deepoxydation state of the xanthophyll cycle (DPS) was significantly affected by temperature ($F_3 = 12.087$, $p < 0.0001$). At 15 °C, DPS is higher than at the other temperature treatments (Fig. 2). Even though there is no strong statistical significance in salinity ($F_1 = 4.478$, $p = 0.0449$),

Fig. 1 Maximum quantum yield (F_v/F_m) of *Laminaria solidungula* during the multiple-stressor experiment with four temperatures (0, 5, 10, 15 °C) and two salinities (S_A 25, 35). The gray background represents the temperature acclimation phase. The white background represents the temperature \times salinity treatment phase. Values are means \pm SD ($n = 4$). Significant differences in final data points are marked with different letters (two-way ANOVA with post hoc Tukey's test; $p < 0.05$)

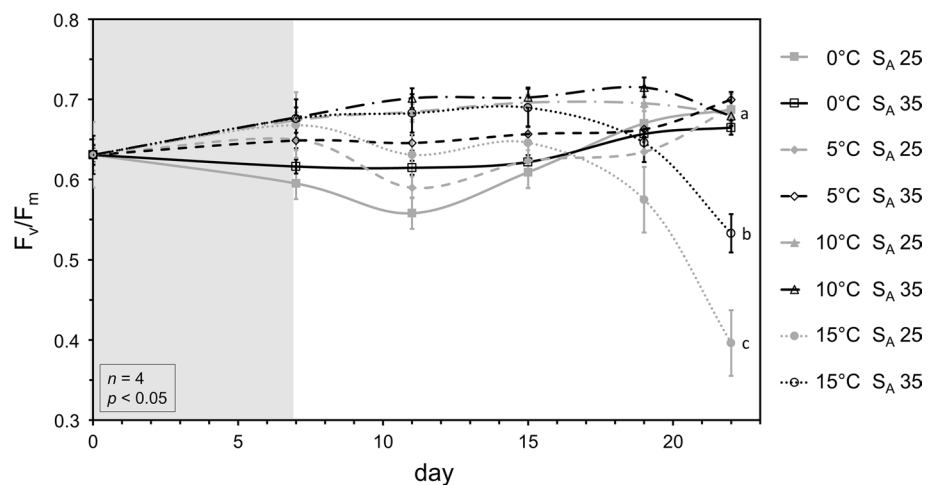


Table 1 Difference in pigment concentration [$\mu\text{g g}^{-1}$ dry weight (DW)] and phlorotannin concentration (mg g^{-1} DW) in *Laminaria solidungula* after a 2-week exposure in a multiple-stressor experiment with four temperatures (0, 5, 10, 15 °C) and two salinities (S_A

25, 35): chlorophyll *a* (Chl *a*), chlorophyll *c*2 (Chl *c*2), fucoxanthin (Fuc), β -carotene (β -Car), and the pool of the xanthophyll cycle pigments (VAZ: violaxanthin, antheraxanthin, zeaxanthin) and soluble phlorotannins

Temp. (°C)	S_A	Chl <i>a</i> ($\mu\text{g g}^{-1}$ DW) ^a	Chl <i>c</i> 2 ($\mu\text{g g}^{-1}$ DW)	Fuc ($\mu\text{g g}^{-1}$ DW) ^a	β -Car ($\mu\text{g g}^{-1}$ DW) ^a	VAZ ($\mu\text{g g}^{-1}$ DW) ^b	Phlorotannins (mg g^{-1} DW)
0	25	602.14 (± 94.29)a	182.84 (± 11.90)a	416.49 (± 58.40)a	77.37 (± 6.04)a	84.99 (± 52.78)c	1.29 (± 0.16)ab
	35	509.75 (± 181.89) abc	156.37 (± 42.05)a	352.31 (± 111.02)a	63.54 (± 13.38)ab	88.14 (± 6.07)bc	1.42 (± 0.12)abc
5	25	551.13 (± 67.98)ab	171.86 (± 13.64)a	395.16 (± 43.84)a	75.35 (± 5.13)ab	75.50 (± 19.56)abc	1.60 (± 0.19)c
	35	512.39 (± 77.36) abc	165.26 (± 10.96)a	370.47 (± 47.86)a	71.17 (± 2.42)ab	55.38 (± 10.24)ab	1.43 (± 0.15)cb
10	25	406.49 (± 55.12)bc	128.88 (± 21.67)a	303.61 (± 41.94)a	59.27 (± 11.40)ab	45.36 (± 17.94)a	1.42 (± 0.13)ab
	35	878.25 (± 206.58)c	202.54 (± 22.19)a	573.65 (± 107.87)a	77.99 (± 7.86)ab	85.86 (± 26.29)c	1.24 (± 0.12)a
15	25	761.35 (± 45.55)bc	171.24 (± 9.59)a	517.91 (± 29.52)a	75.20 (± 4.23)ab	101.24 (± 6.41)c	1.35 (± 0.19)ab
	35	609.79 (± 55.48) abc	170.94 (± 4.15)a	418.52 (± 36.11)a	78.03 (± 2.03)b	92.34 (± 10.72)c	1.20 (± 0.18)a

Significant differences are marked with different letters ($n = 4$; generalized linear model [GLM]; $p < 0.05$; further statistical details in Supplementary Table 1)

^aReciprocal

^b \log_{10} transformation

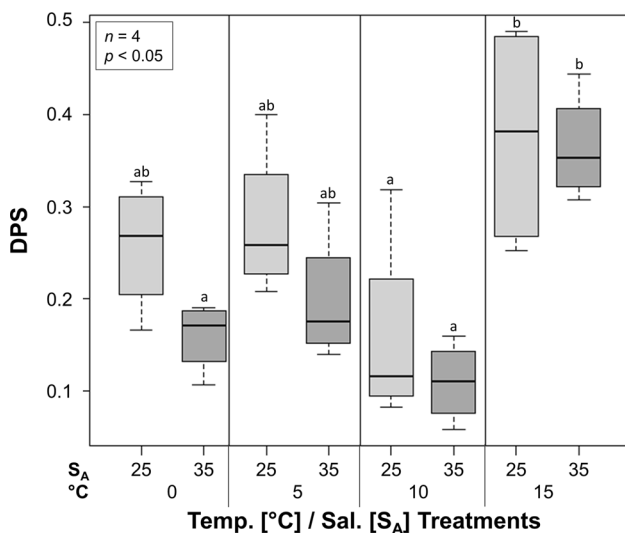


Fig. 2 Deepoxydation state of the xanthophyll cycle (DPS) of *Laminaria solidungula* after a 2-week exposure in a multiple-stressor experiment with four temperatures (0, 5, 10, 15 °C) and two salinities (S_A 25, 35). Significant differences in final data points are marked with different letters ($n = 4$; two-way ANOVA with post hoc Tukey's test; $p < 0.05$)

a clear trend to lower DPS values at S_A 35 can be projected. Hence, DPS is increasing with increasing physical stressors.

Mannitol

Temperature and salinity stress affected the mannitol concentration significantly (Fig. 3), both individually (temperature: $F_3 = 7.038$, $p = 0.0015$; salinity: $F_1 = 79.520$, $p < 0.0001$) and interactively ($F_3 = 79.520$, $p = 0.0027$). Regarding the control salinity treatment (S_A 35), only the 15 °C treatment showed a significant decrease in mannitol from about 1600 (0–10 °C) to $1,323 \pm 78 \mu\text{mol mg}^{-1}$ DW ($n = 4$; 0 °C: $p = 0.0111$; 5 °C: $p = 0.0393$; 10 °C: $p = 0.0266$). The samples incubated at low salinity (S_A 25) generally contained less mannitol than the control salinity samples across all temperatures, with significant differences at 0 °C ($p < 0.0001$) and 5 °C ($p = 0.0002$). Temperature and salinity stress showed an interactive and additive effect on mannitol, since the concentration in samples at S_A 25 increased from 0 to 10 °C. Apparently, temperatures beyond the optimum range limited the alga's ability to compensate salinity differences, resulting in a decrease of mannitol at S_A 35 as well as S_A 25.

Carbon, nitrogen and C:N ratio

The carbon:nitrogen (C:N) ratio (Fig. 4a) was significantly affected by temperature ($F_3 = 280.872$, $p < 0.0001$), salinity ($F_1 = 121.773$, $p < 0.0001$), and by the interaction of

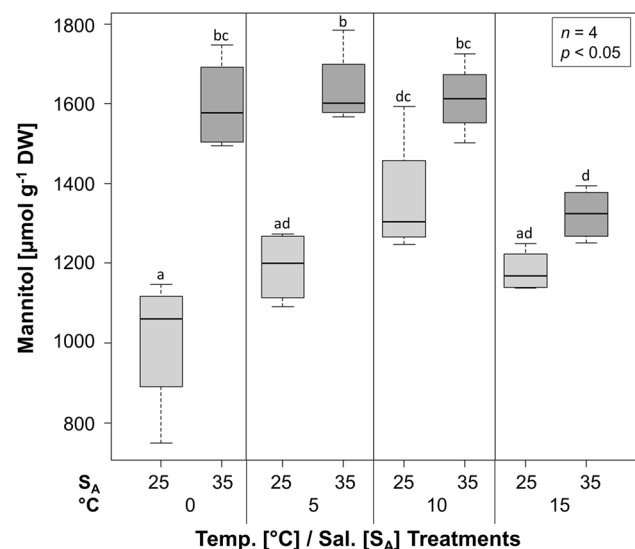


Fig. 3 Mannitol concentration [$\mu\text{mol g}^{-1}$ dry weight (DW)] in *Laminaria solidungula* after a 2-week exposure in a multiple-stressor experiment with four temperatures (0, 5, 10, 15 °C) and two salinities (S_A 25, 35). Significant differences are marked with different letters ($n = 4$; two-way ANOVA with post hoc Tukey's test; $p < 0.05$)

both physical factors ($F_3 = 4.025$, $p = 0.0188$). The results indicated an antagonistic effect of increased temperature and low salinity. With higher temperatures, the C:N ratio was significantly higher. The C:N ratio increased above 20 at 10 and 15 °C at both salinities, while it was below 20 at 5 and 10 °C. Additionally, at each temperature, the C:N ratio at S_A 25 was significantly lower than at the control of S_A 35.

For further exploration, the total C and total N contents were analyzed. Temperature increase ($F_3 = 22.494$, $p < 0.0001$) and salinity decrease ($F_1 = 6.564$, $p = 0.0171$) had each a significant and an interactive antagonistic ($F_3 = 4.341$, $p = 0.0140$) impact on the total N content (Fig. 4c). On the one hand, the total N content decreased at higher temperatures (10, 15 °C) at both salinities. On the other hand, the N concentration increased at S_A 25 at each temperature, compared to the control S_A 35. The total C content (Fig. 4b) barely changed (temperature: $F_3 = 178.729$, $p < 0.0001$; salinity: $F_1 = 78.823$, $p < 0.0001$), with slight changes in the range of 331 ± 14 and $378 \pm 2 \text{ mg g}^{-1}$ DW ($n = 4$). Hence, the increasing C:N ratio was mainly driven by N variations. However, the C content increased at 10 °C/ S_A 35, 15 °C/ S_A 35 and 15 °C/ S_A 25, which balanced out the variation in C:N ratio in these treatments.

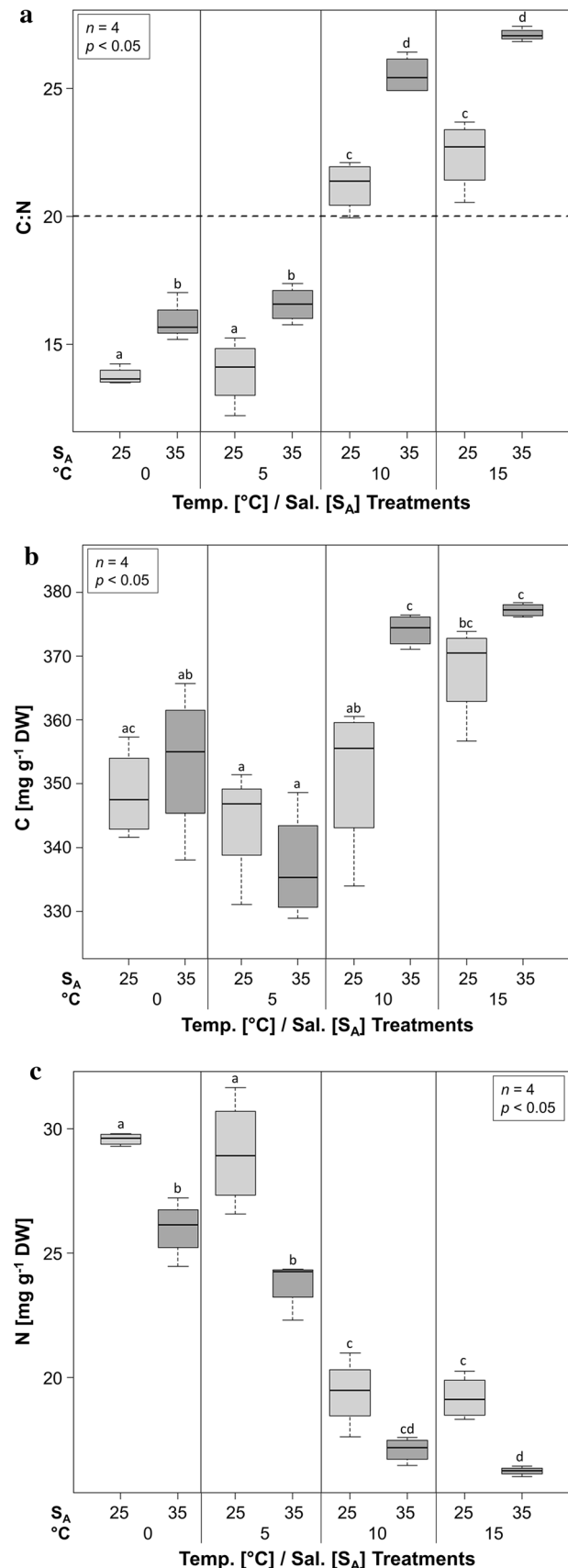
Discussion

The interactive effects of different temperatures and salinities revealed strong physiological and biochemical responses in *Laminaria solidungula* towards a changing environment.

Fig. 4 Carbon (C) and nitrogen (N) content in *Laminaria solidungula* after a 2-week exposure in a multiple-stressor experiment with four temperatures (0, 5, 10, 15 °C) and two salinities (S_A 25, 35). Significant differences are marked with different letters ($n = 4$; two-way ANOVA with post hoc Tukey's test; $p < 0.05$). **a** C:N ratio. The dashed line represents the mean C:N ratio of temperate and tropical seaweeds (Atkinson and Smith 1983). **b** Total carbon (C) concentration [mg g^{-1} dry weight (DW)]. **c**: Total nitrogen (N) concentration [mg g^{-1} DW]

It has been shown in macroalgae before that under multiple-stressor conditions, the effects on the physiological performance and biochemical constituents often either interact in an additive or antagonistic manner (Fredersdorf et al. 2009; Gordillo et al. 2016; Springer et al. 2017). As an Arctic endemic species, *L. solidungula* is adapted to low temperatures (tom Dieck (Bartsch) 1992) and it is characterized as a stenohaline species (Karsten 2007). The present study indeed demonstrated the vulnerability of this species to changes in environmental parameters by exposing it to abiotic conditions beyond the ambient range.

As had been observed before, photosynthetic optimum quantum yield (F_v/F_m) was inhibited by lower salinities and temperature stress (Kirst 1989; Fredersdorf 2009; Nitschke et al. 2014; Ji et al. 2016). Independently of salinity, 15 °C has a major impact on F_v/F_m , resulting in a significant diminishment of the photosynthetic capacity. Temperature-induced stress in the thalli of *L. solidungula* was also reported by Parages et al. (2013). Mitogen-activated protein (MAP) kinase-like proteins, which are involved in stress responses, were rapidly activated at 7 °C. Karsten (2007) hypothesized a temperature-limited physiological capacity of cold-temperate and Arctic species to acclimate to external salinity changes. This hypothesis could be confirmed in this study. The combination of low salinity and for the Arctic extreme temperatures of 15 °C inhibited the photosynthetic activity and diminished the mannitol content of *L. solidungula* significantly. Karsten (2007) showed that the photosynthetic performance can be maintained for a short period of stress, but is affected after continued stress exposure, by comparing quantum yields in several Arctic macroalgae after two and five days of treatment. We were able to confirm this effect, however, the significant decrease of F_v/F_m only occurred after 2 weeks. This shows that *L. solidungula* can compensate stress for a short period but is susceptible if environmental stressors are applied for a longer period. Mannitol is a carbohydrate of low molecular weight and known to play a significant role in the water balance of algal cells (Kirst 1989). Acting as an osmolyte and compatible solute, it preserves the functions of the cells during osmotic stress (Kirst 1989; Eggert et al. 2007). In our experiment, less mannitol was apparently stored in the cells of *L. solidungula* to prevent water flow into the cells under hypoosmotic stress (S_A 25), while at S_A 35 the mannitol



content remained almost unchanged. Nevertheless, in this study an impact of temperature was also observed. Since mannitol is the main photosynthetic product of brown algae, it was affected by temperature (Ji et al. 2016). The optimum growth temperature of *L. solidungula* was determined to be 5–10 °C (tom Dieck (Bartsch) 1992). It is generally known that with increasing temperature the enzymatic processes accelerate, while temperature stress above a certain threshold leads to inhibition of metabolic processes (Graiff et al. 2015b). Accordingly, the mannitol concentration in *L. solidungula* increased at S_A 25 between 0 and 10 °C and decreased at 15 °C, likely being in the range of inhibited metabolic processes.

In contrast to studies by Davison et al. (1991) and Celis-Plá et al. (2014), a dependence of the absolute pigment content on growth temperatures, photosynthetic efficiency or other environmental stressors could not be confirmed in this study (Table 1). Furthermore, contrary to Mannino et al. (2016) and Springer et al. (2017), there was no significant increase or decrease of antioxidants due to stress treatment observed on any level (Table 1).

Even though no changes in the pool-size of xanthophylls (VAZ) were detected, the deepoxydation state (DPS) was significantly affected by temperature and increased at 15 °C. Furthermore, higher DPS in the low salinity treatments was detected. Changes in the xanthophyll cycle and hence the DPS are an important stress response in seaweeds, mainly as protection against photo-oxidative stress (Müller et al. 2001; Goss and Jakob 2010). Li et al. (2019) and Olischläger et al. (2017) detected an increase of DPS at the suboptimal temperatures in *Saccharina latissima* from the Arctic and Helgoland. These two studies and the result of our study support the hypothesis, that stress, such as suboptimal temperatures or hyposalinity, is also compensated by an increasing DPS in seaweeds.

A clear temperature-driven increase of the C:N ratio could not be determined in this study, even though it already has been reported in *L. solidungula* and other polar macroalgae (Dunton and Schell 1986; Gordillo et al. 2006; Graiff et al. 2015a). Nonetheless, at higher temperatures (10 and 15 °C), the C:N ratio was significantly increased than at lower temperatures (0 and 5 °C), showing a general negative impact of high temperatures in *L. solidungula*. Additionally, in contrast to Graiff et al. (2015a) a decrease in C:N ratio, as has been shown in *F. vesiculosus* at very high temperatures, could not be confirmed. Instead, we observed a direct correlation of temperature to the increase in C:N ratio. Atkinson and Smith (1983) showed that benthic marine algae from temperate and tropical regions had a mean C:N ratio of 20, while 10 was considered to be very low and indicative for sufficient N supply. In *L. solidungula*, the C:N ratio increased above 20 at 10 and 15 °C, indicating N limitation (Atkinson and Smith 1983; Peters et al. 2005). With

the analyses of total C and total N, the strong increase in the C:N ratio could be explained by a strong decrease of total N content in the samples. The total C content constitutes all carbohydrates, including all polysaccharides and is affected by the tissue structure (Peters et al. 2005). With changing photosynthetic activity or growth, C assimilation and C utilization can be affected (Gómez and Wiencke 1998; Gevaert et al. 2001). Nevertheless, a clear impact of temperature or salinity on the total C content could not be detected. Contrarily, the amount of total N decreased significantly with increasing temperatures, which means less N is taken up from the medium and stored as organic molecules and amino acids in the tissue (Gevaert et al. 2001). To exclude any effect of the experimental design on the reduced N uptake, sufficient N supply in the medium was ensured. In fact, the N accumulation in *L. solidungula* must therefore be intrinsically inhibited by temperature increase and at control salinity. Decreases in N concentrations might be explained, for example, by decreased nitrate reductase activity, protein synthesis and limited N storage as has been shown by Reay et al. (1999) and Gordillo et al. (2006). An increasing N uptake at lower salinities was previously detected in *Fucus serratus* and explained by an increased N metabolism at lower salinities (Gordillo et al. 2002). Mandal et al. (2015) showed a dependence of temperature and salinity on N uptake in the red alga *Kappaphycus alvarezii*. In land plants, a reduced N uptake was detected in saline soils, due to enhanced chloride concentrations in the soil (Mansour 2000). This fact can also be assigned to seaweed and seawater. Hence, an increasing N metabolism could have led to the higher N concentrations at the low salinity treatments in *L. solidungula*.

In conclusion, salinity and temperature had an additive and antagonistic impact on the Arctic seaweed *L. solidungula*, depending on the analyzed response variable. Concerning photosynthetic processes, *L. solidungula* seems to be well adapted to its Arctic habitat with natural temperature and salinity variations, but being restricted by the extreme temperature of 15 °C. *L. solidungula* tolerated 0–10 °C and could compensate the decreasing salinities at these temperatures, while at 15 °C the osmotic stress at control salinity could not be compensated anymore. Furthermore, this study confirms that abiotic stressors can be compensated for a short period of time (e.g., Karsten 2007; Simonson et al. 2015a). Even though the absolute pigment content was not affected by the two stressors, the DPS increased to compensate rising physiological stress. Regarding mannitol, temperature increase and salinity decrease affected the concentration additively. Suboptimal temperatures resulted in lower mannitol concentrations at low salinity, while the control salinity S_A 35 resulted in higher concentrations independent from temperature. Temperatures exceeding the optimum range limited the alga's ability to compensate salinity differences. Contrary to mannitol, temperature and

salinity had an antagonistic impact on total N and hence the C:N ratio, as increasing temperature resulted in decreasing N content. Nonetheless, S_A 25 could compensate for temperature interferences.

Our results demonstrate the importance of research on physiological and biochemical responses to interactions of two or more environmental stress factors, regarding consequences of climate change. In accordance to the study of Müller et al. (2009) on polar seaweeds under ocean warming, we can confirm that also the combination of several emerging environmental stressors may result in a retreat or even extinction of some *L. solidungula* populations and a shifting into higher Arctic Regions.

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Compliance with ethical standards

Conflict of interest All authors declare that they are free of competing interests.

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