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Photosynthetic response of Arctic kelp zoospores exposed to radiation and thermal stress†

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Zoospores of Arctic kelp species, *Alaria esculenta*, *Laminaria digitata* and *Saccharina latissima* were exposed to different temperature (2 °C to 19 °C) and radiation (photosynthetically active radiation (PAR = P), PAR + UV-A (PA), and PAR + UV-A + UV-B (PAB)) conditions in the laboratory. Species-specific responses to the combined effect of light and temperature stress showed sensitivity in the order *S. latissima* > *L. digitata* > *A. esculenta*. The optimum temperature range for photosynthesis in different Arctic kelp species' zoospores was between 7–13 °C, temperatures higher than in the natural environment. Short-term response to increasing temperature was non-lethal while moderate temperature increase had an ameliorating effect on the overall biological effect of UVR; where the lowest photoinhibition was observed at 13 °C under PAB and higher photosynthetic recovery was observed in UVR-pre-exposed zoospores at 7–13 °C compared to 2 °C. Above the temperature optima, continued cultivation under high temperature had a negative impact on the recovery of photoinhibition. The higher capacity for non-photochemical quenching (NPQ) in *A. esculenta* and *L. digitata* helped to regulate and protect photosynthesis under light and temperature stress compared to *S. latissima.* The investigated Arctic kelp species may be able to locally survive under the influence of UVR at a certain range of temperature increase but the southernmost distribution range of the species may shift to higher latitudes; although natural selection may result in genotypes adapted to stressful environment.

Introduction

The present state of the world climate is marked by continued global warming, further declines in Arctic sea ice and severe stratospheric ozone depletion, especially in the Antarctic; all notable climate anomalies and events occurring in the year 2006.[1] The global climate change, which is anthropogenic in origin, is progressing at an unprecedented speed with a projected increase in global mean temperature of up to 6 °C over this century.[2,3] Moreover, the "Arctic amplification" phenomenon has brought about near-surface warming in the Arctic twice as large as the global average over recent decades.[4,5] Consequently, the decrease in Arctic sea ice cover and surface albedo has altered the solar radiation forcing on the Arctic atmosphere–ice–ocean system allowing more solar heating of the upper ocean.[6]

Various North Atlantic kelp species have broad latitudinal distribution occurring as far south as the 16 °C summer isotherm on the coasts of Brittany and Portugal and extend north towards the Arctic.[7,8] The species-specific temperature tolerance and temperature ranges for survival, growth, and reproduction determine their autecology and biogeography.[9,10] Consequently, changing water temperatures can trigger shifts in their distributional boundaries[11–13] and geographic distribution. On the other hand, development of ecotypes is possible[14] allowing disjunct refuge populations to thrive even in stressful environments.

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A significant depletion of the Arctic ozone layer occurred in some years (*e.g.* 1999–2000, 2001–2002, 2004–2005) during the late winter/spring period (January–April)[15–17] coinciding with the reproductive peaks of most Arctic kelp species. Biologically significant ultraviolet radiation (UVR) can penetrate to 5 m depth in Arctic waters that may change in the future due to the interactions between global warming and ozone depletion.[18] Even under non-depleted ozone conditions, UV-B still presents potential negative impacts to photosynthetic organisms.

When exposed to light intensities exceeding their photosynthetic capacity, regulated thermal dissipation of absorbed light is without question the keystone of photoprotection.[19] Moreover, oxygenic photoautotrophic organisms have evolved a highly specialized repair mechanism that restores the functional status of photosystem II (PSII) and prevents the accumulation of photodamage.[20] UV contributes to further photodamage by inactivation of the oxygen-evolving complex and photochemical reaction centers of the PSII[21] which delays photosynthetic recovery in Arctic kelp zoospores.[22]

The photophosphorylation and electron transport enzymes as well as plastoquinone diffusion enzyme are temperature dependent. Variation in temperature can, therefore, affect the light harvesting efficiency (α, the slope of the initial light-limited region of the photosynthesis–irradiance curve) of phototrophs.[23] The low-temperature limitation of electron transport can cause a reduction in the ability of phototrophs to use light. Consequently, the excess light energy may damage the PSII apparatus resulting in photoinhibition.[23] Conversely, the thermolabile nature of PSII is related to the reduction in photosynthesis at temperatures above temperature optimum.[24] The thermal stability of PSII effectively determines the upper temperature tolerance of photosynthesis.

Temperature can also modify the effects of UVR on photosynthesis by affecting the rate of repair. The ameliorating effects of increased temperature under UVR on phytoplankton have been demonstrated for growth in cyanobacteria, diatoms and natural lake assemblages.[25–28] There are also reports showing the beneficial effects of increased temperature on the germination rate, cell number, photosynthesis (F_v/F_m), and DNA damage repair rates of macroalgae.[29–32]

Zoospore germination in the Arctic population of *Alaria esculenta*, *Laminaria digitata* and *Saccharina latissima* was optimal between 2 and 12 °C, and impaired at 18 °C.[33] Significant additional negative UV-B effect was observed at 2 and 12 °C in *L. digitata* and at 12 °C in *S. latissima*, but not in *A. esculenta.*[33] Whether the temperature optima for photosynthesis are the same or higher than the optimum temperatures for growth (or germination) in different Arctic kelp zoospores is yet to be studied. This study aims to determine: (a) the light harvesting efficiency and short-term response of Arctic kelp zoospore photosynthesis to increasing temperature; (b) the role of temperature on photoinhibition and recovery of photosynthesis under PAR and UVR; and (c) the photoprotective function of non-photochemical quenching processes in thermal dissipation. The results are discussed with respect to possible changes in geographic distribution of the studied species.

Experimental

Materials and methods

Algal material. Fertile sporophytes of *Alaria esculenta* (Linnaeus) Greville, *Laminaria digitata* (Hudson) Lamouroux and *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders were collected between May and June 2006 by SCUBA divers in Kongsfjorden at Prins Heinrichøya or Blomstrandhalvøya close to Ny Ålesund (Spitsbergen, 78° 55′ N, 011° 56′ E). Blades with sori were excised from five different individuals per species (representing the five replicates), cleaned of epiphytes, blotted with tissue paper and kept in darkness in a moist chamber at 0 °C overnight for a maximum of 2 days. To induce rapid release of zoospores, sori were immersed in 5–10 ml filtered (0.2 µm pore size) seawater at ±15 °C and exposed to natural light close to a window. Initial density of zoospores in all experimental units was standardized by measuring initial Chl *a* fluorescence (F_0) between 800–1000 mV. Stock suspensions were diluted with filtered seawater to obtain the desired fluorescence among the five replicates.

Temperature-controlled rooms and radiation treatments

Four temperature-controlled rooms were established at 2°, 7°, 13° and 19 °C. Inside each chamber, white fluorescent tubes (Osram, L65 Watt/25S, Munich, Germany) and UVA-340 fluorescent tubes (Q-Panel, Cleveland, OH, USA) were used to provide photosynthetically active radiation (PAR, 400–700 nm) and ultraviolet radiation (UVR, 280–400 nm), respectively. To cut off different wavelength ranges from the spectrum emitted by the fluorescent tubes, cell culture dishes were covered with one of the following filters: Ultraphan transparent (Digefra GmbH, Germany), Folanorm (Folex GmbH, Germany) or Ultraphan URUV farblos corresponding to the PAR + UV-A + UV-B (PAB), PAR + UV-A (PA) and PAR (P) treatments, respectively. Ultraviolet radiation was measured using a Solar Light PMA 2100 radiometer equipped with the UV-A sensor PMA 2110 and the UV-B Sensor PMA 2106 (Solar Light, Philadelphia, USA). Adjusted ultraviolet radiation below the cut-off filters was 4.34 W m^{-2} UV-A and 0.40 W m^{-2} UV-B. The available PAR measured using a cosine quantum sensor attached to a LI-COR data logger (LI-1000, LI-COR Biosciences, Lincoln, Nebraska, USA) was 22 µmol photons m^{-2} s^{-1} (~4.73 W m^{-2}). The maximum daily average irradiance in air in summer (June and July) is 790 µmol photons m^{-2} s^{-1} PAR, 17 W m^{-2} UV-A and 0.30 W m^{-2} UV-B.[34]

Chlorophyll fluorescence measurements

Photosynthetic efficiencies of zoospores were measured as variable fluorescence of PSII using a Water Pulse Amplitude Modulation fluorometer (Water-PAM) consisting of Emitter-Detector Unit Water-ED and PAM-Control Universal Control Unit connected to a PC operated with WinControl software (Heinz Walz GmbH, Effeltrich, Germany).[22] Immediately after adjustment of spore density, the suspension was filled into the 5 ml quartz cuvettes and the optimum quantum yield (F_v/F_m) was measured inside the Emitter-Detector Unit at time zero ($n = 5$). After 3 min of dark incubation, F_0 was measured with a red measuring light pulse (~0.3 µmol photons m^{-2} s^{-1}, 650 nm), and F_m was determined with a 800 ms completely saturating red light pulse (~2750 µmol photons m^{-2} s^{-1}, 650 nm).

Rapid photosynthesis (in terms of relative electron transport rate, rETR = PFR × $\Delta F/F_m'$) *versus* irradiance (E) curves (P-E curve) of zoospore suspension were measured in triplicates using a Water PAM device (Walz, Effeltrich, Germany) described by Roleda *et al.*[22] Samples were exposed to actinic light for 30 s at each of 8 points of increasing intensity (4–69 µmol photons m^{-2} s^{-1}). The hyperbolic tangent model of Jassby and Platt[35] was used to estimate P-E curve parameters described as:

$$\mathrm{rETR} = \mathrm{rETR}_{max} \times \tanh(\alpha \times E_{PAR} \times \mathrm{rETR}_{max}{}^{-1})$$

where rETR_{max} is the maximum relative electron transport rate, tanh is the hyperbolic tangent function, α is the electron transport efficiency and E is the photon fluence rate of PAR. Curve fit was calculated with the Solver Module of MS-Excel using the least squares method comparing differences between measured and calculated data. The saturation irradiance for electron transport (E_k) was calculated as the light intensity at which the initial slope of the curve (α) intercepts the horizontal asymptote (rETR_{max}).

Controls measured at time zero were filled into corresponding culture dishes (35 mm × 10 mm; CorningTM, Corning Inc., NY, USA). To evaluate the effect of different radiation treatments (3 levels: P, PA and PAB) under different temperatures (4 levels: 2°, 7°, 13° and 19 °C), samples of fresh zoospore suspension (not exceeding 1 h after release) were filled into each culture dishes. Samples corresponding to the 5 replicates were exposed to each treatment combination for 8 h. After treatment, F_v/F_m was determined and the suspension was returned to the same culture dish and cultivated under dim white light (10 ± 1 µmol photons m^{-2} s^{-1}) at the same temperature for recovery. The controls were also maintained at the same dim light condition and F_v/F_m was repeatedly measured in time-series. Measurements of photosynthetic

recovery of high PAR and UVR-treated samples were made after 48 h in dim light condition. The non-photochemical-quenching (NPQ) parameter after exposure to different combination of temperature and light treatments was derived according to the equation: $NPQ = (F_m - F_m')/F_m'$. Settled and germinating spores were slowly resuspended by sucking and jetting the medium against the bottom of the culture dish using Eppendorf pipettes.

Statistical analysis

Raw absolute data were tested for homogeneity (Levene Statistics) of variance. Corresponding transformations (square roots) were made to heteroskedastic data. F_v/F_m were tested using analyses of variance (ANOVA, $P < 0.05$) followed by Duncan's multiple range test (DMRT, $P < 0.05$). Statistical analyses were performed using SPSS software (Chicago, IL, USA).

Results

The rapid photosynthesis–irradiance (P-E) curve parameter estimates of freshly-released zoospores measured in 7 °C temperature-controlled room showed comparable $rETR_{max}$ (ANOVA, $P = 0.603$), α ($P = 0.333$) and E_k ($P = 0.394$) between different kelp species (Fig. 1); with values ranging between 0.66–1.20 rel. units, 0.08–0.16, and 9–16 μmol photons m^{-2} s^{-1}, respectively. After 4 h incubation of zoospores of *Saccharina latisssima* at 2°, 7° and 13 °C, a temperature-dependent variation in light harvesting efficiency and electron transport were observed between treatments (Fig. 2, Table 1). Analysis of variance with individual source sporophytes as a random variable showed temperature and sporophyte-specific variation in $rETR_{max}$ and α (ANOVA, $P < 0.05$) but not the E_k (ANOVA, $P > 0.05$). The $rETR_{max}$ and α were highest in 13 °C (1.6 ± 0.8 and 0.1 ± 0.04, respectively) and lowest in 2 °C (0.6 ± 0.3 and 0.04 ± 0.02, respectively).

The optimum quantum yield of zoospores for up to 48 h after release and subsequent incubation at different temperature under low white light (10 μmol photons m^{-2} s^{-1}) showed decreasing F_v/F_m in all species at 19 °C with *L. digitata* and *S. latissima* showing adverse response already after 4 h and 8 h incubation, respectively (Fig. 3). Optimum F_v/F_m was measured at 13 °C in all species. The F_v/F_m measured at 2 °C was compromised but sustained at a minimum up to 48 h. Conversely, F_v/F_m progressively decreased at 19 °C, with <50% yield after 24 h in all species and <75% to non detectable in *S. latissima* after 48 h incubation. Repeated measure analysis of variance (RMANOVA, $P < 0.05$) showed significant differences between species, temperature and their interaction. The Posthoc Duncan's multiple range test (DMRT, $P = 0.05$) showed species-specific photosynthetic performance in kelp zoospores, *A. esculenta* (*Ae*) > *L. digitata* (*Ld*) > *S. latissima* (*Sl*) while optimum photosynthesis temperature was at 13 °C > 7 °C > 2 °C > 19 °C.

Table 1 Individual sporophyte-specific vitality in *Saccharina latissima* impacts the maximum photosynthetic electron transport rate ($rETR_{max}$), and light harvesting and photosynthetic conversion efficiency (α) of their respective zoospores after 4 h acclimation to different culture temperature

		Temperature		
P-E parameter	Sporophyte	2 °C	7 °C	13 °C
$rETR_{max}$	1	0.404	0.614	0.985
	2	0.880	2.057	2.571
	3	0.482	1.089	1.352
α	1	0.023	0.076	0.080
	2	0.053	0.108	0.145
	3	0.038	0.074	0.086
E_k	1	17.5	8.1	12.3
	2	16.6	19.1	17.8
	3	12.6	14.8	15.8

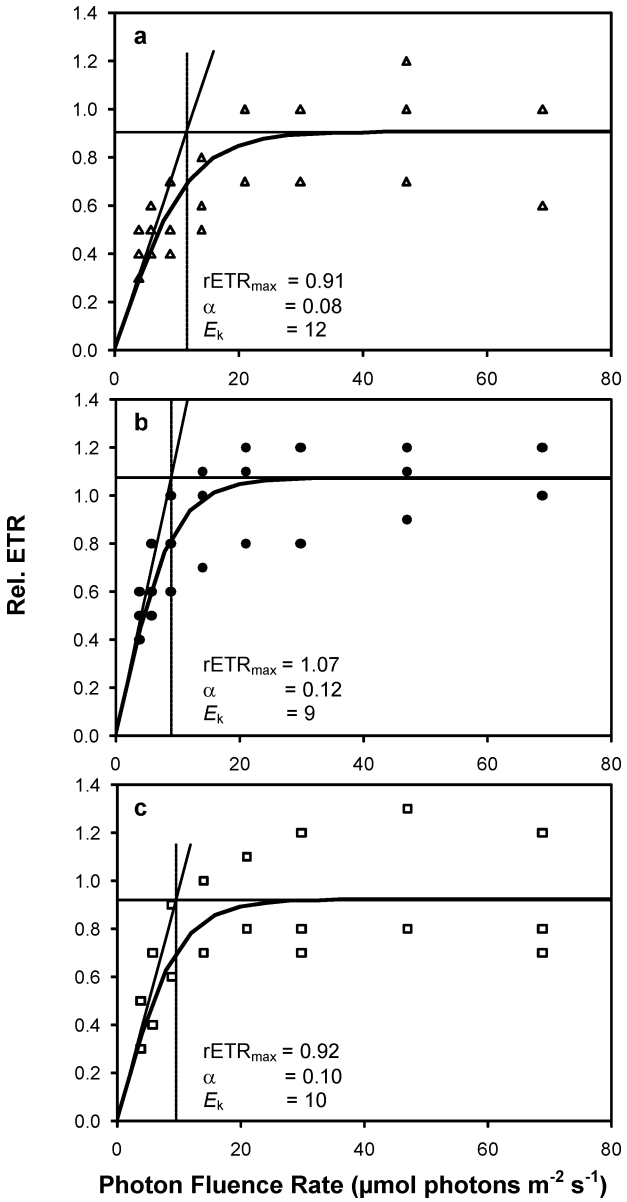

Fig. 1 Rapid light curves (photosynthesis–irradiance, P-E curves) of zoospores in (a) *Alaria esculenta*, (b) *Laminaria digitata* and (c) *Saccharina latissima* ($n = 3$) immediately after release from the sori. PFR is the respective photon fluence rate of actinic light (30 s exposure) and rETR is the relative electron transport rate, an index of light harvesting and subsequent charge separation in PSII and PSI initiating electron transport and production of NADPH and ATP. Saturating irradiance (E_k) is estimated as the point at which the initial slope (α) crosses maximum photosynthesis ($rETR_{max}$) using the hyperbolic tangent model of Jassby and Platt, 1976.[35] Thick solid lines are the calculated mean curve fit for each species.

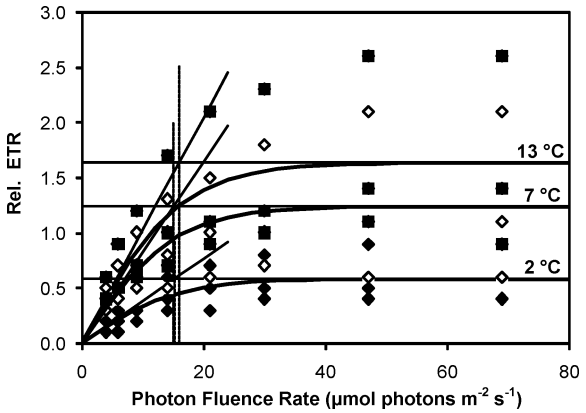

Fig. 2 Rapid light curves (photosynthesis–irradiance, P-E curves) of *Saccharina latissima* zoospores after 4 h incubation at different temperatures (2 °C ◆, 7 °C ◇, and 13 °C ■) maintained under low white light (10 µmol photons m^{-2} s^{-1}). PFR is the respective photon fluence rate of actinic light and rETR is the relative electron transport rate. Thick solid lines are the mean curve fits for each temperature treatment calculated using the hyperbolic tangent equation. Spread of measured data points revealed individual-specific vitality of zoospores released from each sporophyte as shown in Table 1.

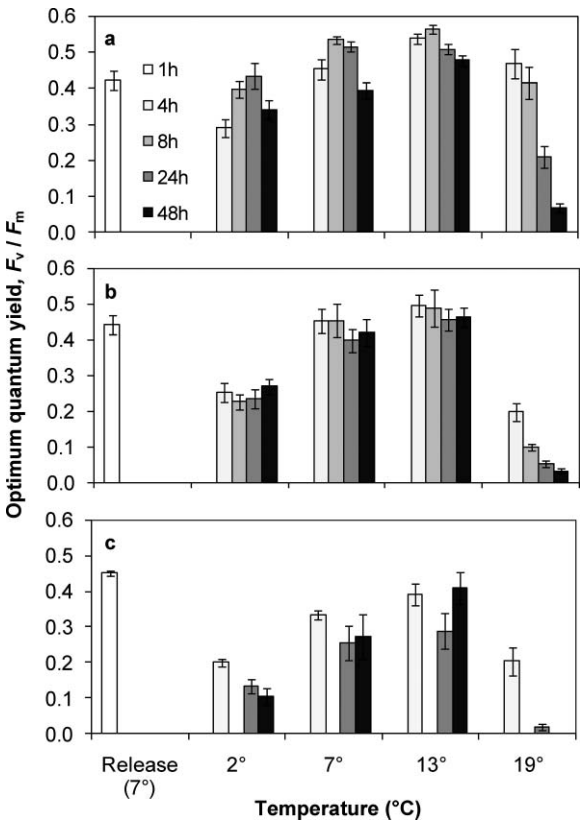

Fig. 3 Time series measurements on the mean optimum quantum yield (F_v/F_m) of zoospores in (a) *Alaria esculenta*, (b) *Laminaria digitata* and (c) *Saccharina latissima* cultivated in different temperatures under low PAR (10 µmol photons m^{-2} s^{-1}). Error bars are SEs ($n = 5$). Repeated measure analysis of variance, RMANOVA, is shown in Table 3.

Exposure to different combination of experimental light and temperature treatments depressed the F_v/F_m in all species after 8 h incubation (Table 2). Generally, F_v/F_m was lowest at 2 °C and at all temperature regimes under the whole light spectrum (PAB). Photosynthetic performance expressed as percent photoinhibition showed highest inhibition of photosynthesis at 2 °C in all kelp species under all light treatments (Fig. 4a–c). Under P treatment, photoinhibition decreased with increasing temperature in *A. esculenta* (Fig. 4a). In *L. digitata* and *S. latissima*, photoinhibition was lowest at 13 °C (Fig. 4b, c). Photoinhibition under PA was highest at the temperature extremes, 2 °C and 19 °C, in both *L. digitata* and *S. latissima*; while *A. esculenta* was more photoinhibited at the lower temperature extreme. A similar trend was observed under PAB in all species but with relatively lower photoinhibition at 13 °C compared to other temperatures.

Photosynthetic recovery was observed after exposure treatment and 48 h post-cultivation under low white light (Fig. 4d–f). Recovery was highest in germlings of *A. esculenta* (78–112%) and *L. digitata* (73–100%) cultivated at 7 °C and 13 °C regardless of pre-exposure light treatment (Fig. 4d, e). At the same cultivation temperatures, *S. latissima* germlings recovered only 44–66% after exposure to P and PA, and 22–26% after PAB pre-exposure (Fig. 4f). At 2 °C cultivation temperature, *A. esculenta* recovered 57–59% in P- and PA-pre-exposed zoospores compared to only 30% in PAB-pre-exposed zoospores; lower recovery was observed in *L. digitata* at 38–46% and 10% and in *S. latissima* at 15–18% and 6%, respectively. At 19 °C, minimal recovery was observed in all species regardless of the pre-exposure light treatment ranging from 8–14% in *A. esculenta* and 2–5% in *L. digitata* to non-detectable in *S. latissima.* Analysis of variance (2-way ANOVA, $P < 0.05$) showed a significant effect of the main factors (temperature and radiation) on the F_v/F_m after exposure and recovery in all species investigated and their interaction in *A. esculenta* and *L. digitata* (Table 3). The Posthoc Duncan's multiple range test (DMRT, $P = 0.05$) showed a general species-specific sensitivity to experimental radiation and temperature treatments, $Sl > Ld > Ae$; while the capacity to recover PSII function was highest in $Ae = Ld > Sl$. The cumulative negative effect of different light spectra on F_v/F_m among the three kelp species was highest in PAB > PA > P; while the effect of radiation treatment on photosynthetic recovery was still evident and measured lowest F_v/F_m in PAB < PA = P after 48 h under low white light. The effect of temperature on PSII function, after 8 h exposure to different radiation treatments among the three species, measured lowest F_v/F_m at 2 °C < 7 °C = 19 °C < 13 °C. Continued cultivation under high temperature had a negative impact on the recovery process where F_v/F_m after 48 h was lowest at 19 °C < 2 °C < 7 °C < 13 °C.

The capacity for non-photochemical quenching (NPQ) was generally highest in *L. digitata* and lowest in *S. latissima* (Fig. 5). NPQ in *A. esculenta* increased with temperature and relative to the total fluence of P, PA and PAB (Fig. 5a). Conversely, NPQ in *L. digitata* was not significantly different between samples exposed to 8 h of different treatment combination (light × temperature) and to that of 8 h control at 19 °C (Fig. 5b). Available data in *S. latissima* after 4 h cultivation in low white light and after 8 h exposure treatment showed limited capacity for non-photochemical quenching (Fig. 5c). After 48 h post-cultivation in low white light, NPQ in germlings of *A. esculenta* and *L. digitata* pre-exposed to higher PAR and UVR decreased in samples grown at 2 °C, 7 °C and 13 °C but not in 19 °C (Fig. 5d, e); while the capacity for NPQ increased in control samples. Generally, the

Table 2 Mean absolute values (±SD) of spore photosynthetic efficiency (optimum quantum yield, F_v/F_m) after 8 h exposure treatment to photosynthetically active radiation (PAR = P); PAR + UV-A radiation (PA); PAR + UV-A + UV-B radiation (PAB) and after 48 h post-cultivation for photosynthetic recovery under different temperature regime

		Optimum quantum yield (F_v/F_m)						
			After exposure			After recovery		
Species	T/°C	Control (t_0)	P	PA	PAB	P	PA	PAB
A. esculenta		0.421 ± 0.054						
	2		0.026 ± 0.006	0.019 ± 0.003	0.013 ± 0.006	0.281 ± 0.041	0.271 ± 0.049	0.142 ± 0.034
	7		0.053 ± 0.008	0.028 ± 0.004	0.022 ± 0.010	0.398 ± 0.032	0.434 ± 0.020	0.370 ± 0.029
	13		0.093 ± 0.013	0.045 ± 0.009	0.038 ± 0.010	0.451 ± 0.050	0.533 ± 0.030	0.457 ± 0.009
	19		0.116 ± 0.010	0.045 ± 0.007	0.025 ± 0.009	0.064 ± 0.019	0.042 ± 0.014	0.037 ± 0.019
L. digitata		0.442 ± 0.056						
	2		0.030 ± 0.008	0.022 ± 0.005	0.017 ± 0.009	0.211 ± 0.038	0.178 ± 0.060	0.046 ± 0.016
	7		0.062 ± 0.010	0.028 ± 0.006	0.027 ± 0.004	0.445 ± 0.074	0.438 ± 0.054	0.339 ± 0.066
	13		0.071 ± 0.010	0.040 ± 0.006	0.029 ± 0.003	0.453 ± 0.062	0.461 ± 0.060	0.351 ± 0.096
	19		0.055 ± 0.008	0.022 ± 0.006	0.017 ± 0.010	0.021 ± 0.017	0.008 ± 0.011	0.006 ± 0.009
S. latissima		0.450 ± 0.015						
	2		0.026 ± 0.006	0.025 ± 0.010	0.011 ± 0.004	0.076 ± 0.056	0.060 ± 0.053	0.024 ± 0.011
	7		0.040 ± 0.012	0.028 ± 0.008	0.021 ± 0.007	0.252 ± 0.105	0.182 ± 0.140	0.108 ± 0.109
	13		0.059 ± 0.005	0.027 ± 0.003	0.027 ± 0.004	0.269 ± 0.130	0.254 ± 0.151	0.091 ± 0.086
	19		0.044 ± 0.018	0.021 ± 0.003	0.013 ± 0.007	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000

Photon flux density is 22 µmol photons m^{-2} s^{-1} (~4.73 W m^{-2}). Photosynthetic recovery was initiated in dim white light of 10 µmol photons m^{-2} s^{-1} after treatment. Control at time zero (t_0) was measured after spore release.

Table 3 Analysis of variance (repeated measure, RMANOVA, and two-way ANOVA) and significance values for the main effects and interactions of independent variables on photosynthetic efficiency in spores of *Alaria esculenta*, *Laminaria digitata* and *Saccharina latissima* (* significant; ns, not significant)

Experiment/variable	Source of variation	SS (W)	df	F value	P value
Temperature					
F_v/F_m	Species (A)	0.830	2	68.412	< 0.001*
	Temperature (B)	2.797	3	153.693	< 0.001*
	A × B	0.160	6	4.402	0.002*
Temperature × radiation					
F_v/F_m (after treatment)	Species	0.032	2	3.851	0.023*
Alaria esculenta	Temperature (A)	0.019	3	90.968	< 0.001*
	Radiation (B)	0.025	2	181.510	< 0.001*
	A × B	0.010	6	23.613	< 0.001*
Laminaria digitata	Temperature (A)	0.005	3	27.936	< 0.001*
	Radiation (B)	0.012	2	107.596	< 0.001*
	A × B	0.002	6	5.345	< 0.001*
Saccharina latissima	Temperature (A)	0.013	3	7.371	0.001*
	Radiation (B)	0.033	2	27.382	< 0.001*
	A × B	0.006	6	1.565	0.201ns
F_v/F_m (after recovery)	Species (A)	1.274	1	13.668	< 0.001*
Alaria esculenta	Temperature (A)	2.059	3	555.908	< 0.001*
	Radiation (B)	0.053	2	21.395	< 0.001*
	A × B	0.051	6	6.843	< 0.001*
Laminaria digitata	Temperature (A)	3.116	3	320.887	< 0.001*
	Radiation (B)	0.162	2	25.089	< 0.001*
	A × B	0.074	6	3.798	0.004*
Saccharina latissima	Temperature (A)	0.951	3	27.391	< 0.001*
	Radiation (B)	0.114	2	4.936	0.016*
	A × B	0.058	6	0.833	0.556ns

Radiation treatments consist of photosynthetically active radiation (PAR = P), PAR + UV-A (PA) and PAR + UV-A + UV-B (PAB). SS (W), within group variation; df (= n − 1), degree of freedom; F, ratio of the model mean square to the error mean square which refers to the data distribution; P value, level of significance of the statistical test.

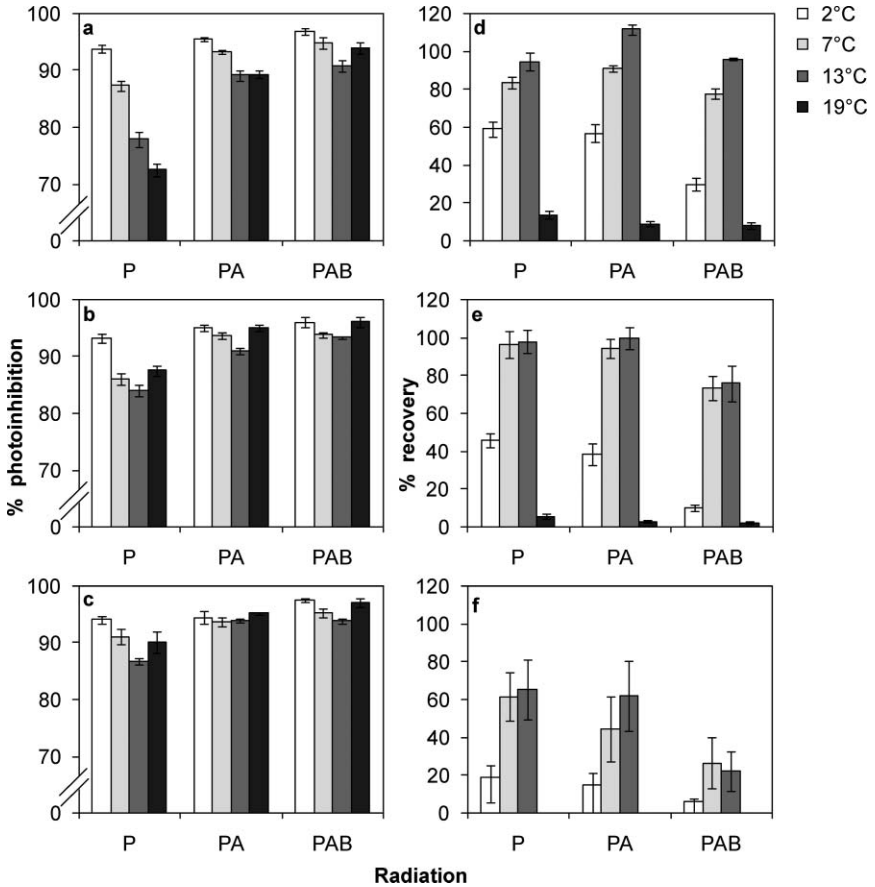

Fig. 4 Mean photoinhibition of photosynthesis after 8 h exposure to photosynthetically active radiation (PAR = P), PAR + UV-A (PA) and PAR + UV-A + UV-B (PAB) at different temperatures in (a) *Alaria esculenta*, (b) *Laminaria digitata* and (c) *Saccharina latissima* expressed as percentage of control (F_v/F_m after release). Corresponding photosynthetic recovery (d, e and f, respectively) after 48 h post-culture in dim white light (10 µmol photons m^{-2} s^{-1}) expressed as percent of control (maximum F_v/F_m at 13 °C). Vertical bars are standard errors (SE, $n = 5$). No photosynthetic recovery was observed under 19 °C in *S. latissima.* Corresponding analysis of variance, ANOVA is shown in Table 3.

capacity for NPQ in *S. latissima* also increased after 48 h post-cultivation; PSII function and NPQ was not detectable at 19 °C cultivation temperature (Fig. 5f).

Discussion

Photosynthetic performance of zoospores from Arctic kelp population was promoted at temperatures higher than in the natural environment. Moreover, photoinhibition of photosynthesis was higher at lower temperature (2 °C) regardless of the spectral irradiance composition compared to temperature near ambient in the natural environment (7 °C) and maximum spring-time cold temperate seawater temperature (13 °C). Zoospores were able to sustain 50% of PSII function at 19 °C up to 24 h in *Alaria esculenta* and only 4 h in *Laminaria digitata* and *Saccharina latissima.* The capacity for photosynthetic recovery was highest at 13 °C in *A. esculenta*; comparable at 7 °C and 13 °C in *L. digitata* and also in *S. latissima* but at a lower range. Photosynthetic recovery was further depressed at extreme low and high temperatures in zoospores previously exposed to the whole UVR spectrum; zoospores of *S. latissima* were most susceptible and *A. esculenta* were more tolerant to the combined UV-B and temperature stress. Generally, the higher capacity for non-photochemical quenching (NPQ) in *A. esculenta* and *L. digitata* helped regulate and protect photosynthesis under light and temperature stress compared to *S. latissima.*

Under a warmer climate scenario in the Arctic, with a realistic temperature increment, the photosynthetic performance (this study) and germination capacity[33] under UVR of some kelp species with wide geographic distribution may not be as severely affected as theoretically projected. Light and temperature may, however, affect the Arctic endemic *Laminaria solidungula*; its zoospores and gametophytes are more susceptible to high radiation and high temperature stress than the investigated species[36,37] and sporophytes grow rapidily in winter under thick ice cover.[38] Moreover, the reproduction of the "rare and localized endemic" Arctic *Saccorhiza dermatodea*[39] can also be compromised as maturation of gametangia requires 6 weeks of exposure to 0 °C.[40,41]

Thermal and photoacclimation of photosynthesis in the sporophytes of panoceanic[39] *Saccharina latissima* (previously *Laminaria saccharina*) had been previously reported.[23,42–44] The increase in photosynthetic efficiency (α) with increasing temperature in zoospores (this study) was also reported in sporophytes of the same species, associated with the increase in Chl *a* and functional PSII reaction centers.[43,44] The increasing F_v/F_m was observed at cultivation temperatures up to 13 °C; a response also consistent

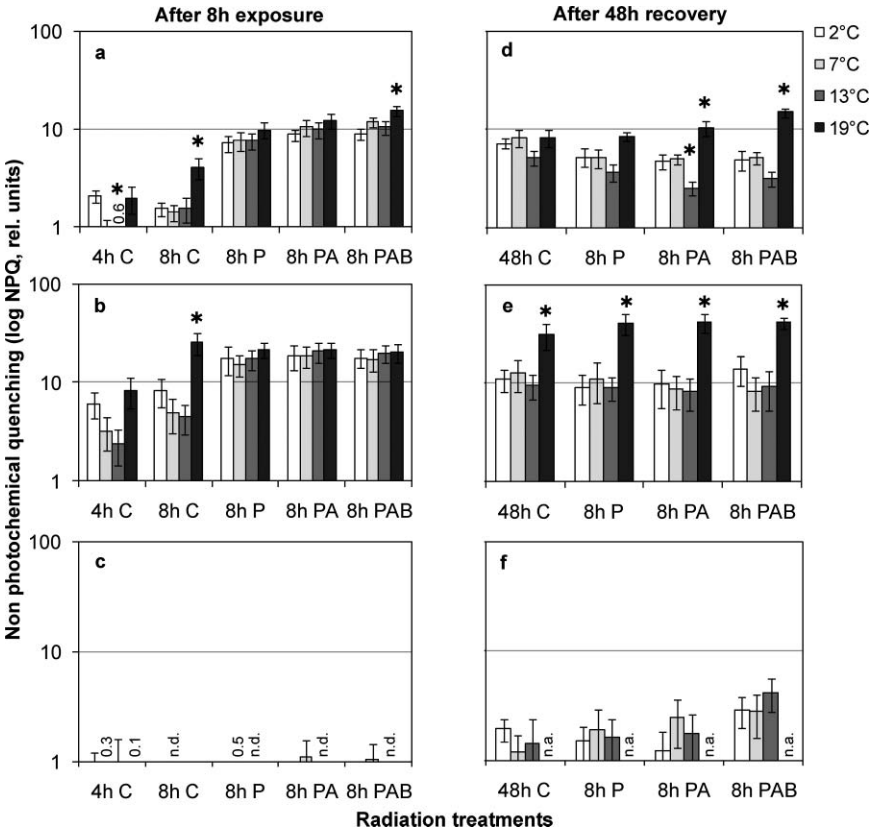

Fig. 5 Non-photochemical quenching (NPQ) as a function of temperature and radiation treatment in zoospores of (a, d) *Alaria esculenta*, (b, e) *Laminaria digitata* and (c, f) *Saccharina latissima* after exposure treatment and post-culture in dim white light (10 µmol photons m^{-2} s^{-1}). Radiation treatments consist of photosynthetically active radiation (PAR = P), PAR + UV-A (PA) and PAR + UV-A + UV-B (PAB) at different culture temperatures. Control (C) was measured after 4, 8 and 48 h incubation in respective temperature chambers under dim white light. Vertical bars are standard errors (SE, $n = 5$). No available data (n.d.) for *S. latissima* at 8 h C, and under 2, 13 and 19 °C after exposure treatments. PSII function and NPQ were non-detectable (n.a.) after 48 h in 19 °C- cultivated *S. latissima.* Analysis of variance (ANOVA, $P < 0.05$) and Post-hoc test (DMRT, $P = 0.05$) showed with * significantly vary from the group.

with previous data for *S. latissima* sporophytes measuring higher maximum photon yield (O_2 evolved per absorbed photon, Φ_{max}, an indicator of F_v/F_m) when grown at high temperature as opposed to low temperature.[43]

The F_v/F_m measured after 8 h at low temperature (LT; 2 °C) and high light (HL; treatment, 22 µmol photons m^{-2} s^{-1}) was lower compared to the same temperature at low light (LL; control, 10 µmol photons m^{-2} s^{-1}) in *A. esculenta* (LT/HL = 0.026; LT/LL = 0.392) and *L. digitata* (LT/HL = 0.030; LT/LL = 0.225). The reductions in F_v/F_m in zoospores grown at LT/HL was due to an increase in energy dissipation away from PSII, *i.e.* non-photochemical quenching; an inverse response of low F_v/F_m and high NPQ was observed in this study (Fig. 5a, b), suggesting that algae grown under low-temperature/high-light conditions can be exposed to potentially damaging excess light energy.[44] Low temperature can inhibit electron transport through alterations in the biophysical properties of thylakoid lipids increasing membrane viscosity and by strongly decreasing the rates of the enzymatic reactions involved in C, N and S reduction than they inhibit photophysical and photochemical processes involved in light absorption, energy transfer and transformation.[45,46]

Conversely, the short-term response to high temperatures and "higher" irradiance of PAR (relative to control) appear to enhance the protective mechanism where percent photoinhibition was lower at higher temperature (Fig. 4a–c), but disrupt repair processes (Fig. 4d–f). The low photoinhibition of zoospores studied at temperatures higher than ambient was unexpected. Photoinhibition is usually enhanced at high temperatures because PSII, and the thylakoids in general, are temperature sensitive.[23] The same response was also reported on the photosynthetic performance of *S. latissima* sporophytes unaffected by higher temperature up to 22 °C.[47] The short exposure period (8 h in this study) might account for lack of high-temperature enhancement of photoinhibition. The decline of photosynthesis at 19 °C was, however, observed after 48 h post-cultivation. Moderate heat stress can stimulate dark reduction of plastoquinone and cyclic electron flow in the light, increase thylakoid leakiness, deactivate rubisco and increase H_2O_2 production. Surprisingly, moderate heat stress is reported to result in little or no damage to PSII even though photosynthetic rate is reduced to near zero.[48] Altering thylakoid lipid composition enables plants to withstand moderately high temperature. The deactivation of rubisco at moderately high temperature is thought to be a parallel deleterious effect or a regulatory response to limit damage to thylakoid reactions.[48] On the other hand, the cellular sites and rates of reactive oxygen species (ROS) production during temperature stress play a central role in stress perception and protection.[49]

Photosynthetic efficiency of spores after exposure treatments decreased to fluorescence ratios below 0.1 (Table 2), which may not be reliable anymore. Despite the methodological limitation, the measured F_v/F_m values were coherent among replicates and treatments (radiation × exposure time) so that an additional UV-effect can be assumed.

Fluorescence data and mean F_v/F_m measured in this study was comparable to that of a previous study on zoospores of the same kelp species exposed to similar experimental irradiance of P, PA and PAB at 7 °C.[22] Moreover, photosynthetic performance at 13 °C in zoospores of Arctic *L. digitata* and *S. latissima* measured F_v/F_m, comparable to that of the cold-temperate population of the same species cultivated at 10 °C after exposure to corresponding irradiance.[50] Recovery of photoinhibition was also comparable between populations of the two species except for the two-fold better recovery process in PAB-exposed Arctic *L. digitata* zoospores at 13 °C (this study) compared to PAB-exposed Helgolandic *L. digitata* at 10 °C.[50] Zoospore germination was also higher in the Arctic population of *L. digitata* compared to Helgolandic population exposed to the whole light spectrum at all temperature except at 18 °C.[33] An opposite trend was observed in *S. latissima* where the Helgolandic population was more tolerant to the combined temperature and light stress compared to the Arctic population.[33]

Population-specific response in *S. latissima* sporophytes was also observed between the population at the southern end of the species' geographic range in the North Atlantic and the population from the higher latitude. The southern population was able to survive higher temperature compared to the northern population[51], indicating natural selection in an unfavorable environment may result in genotypic variation. Based on genetic and fossil evidence, the laminarians are evolving rapidly.[8,52] It is likely that Laminariales together with Desmarestiales and Fucales evolved at a time when there were no significant low-temperature (<5 °C) surface seawaters[53,54] until the Antarctic cooled some 15 Ma ago. Despite this, many of the present dominant macroalgae in cold seas are large brown seaweeds, and many laminarians cannot reproduce at temperatures above 18–25 °C.[55] Recent molecular evidence[56] supports the view that a *Laminaria* ancestor from the North Pacific entered the Arctic and North Atlantic during the latest Pliocene or Pleistocene with rapid spread and speciation in the Atlantic.[39] Aside from traditional evolutionary theory that natural selection occurs among individuals produced sexually, somatic mutation, mitotic recombination, ploidy changes and rapid changes in genotype have all been documented in clonal lineages of macroalgae.[57]

Under a combined action of light and heat stress, strong light induces photodamage of PSII due to the direct action of light on the oxygen-evolving complex while production of ROS, such as H_2O_2, significantly increases with the rise in temperature.[58] Stress-induced accumulation of ROS leads to inhibition of the recovery of the PSII by suppressing the *de novo* synthesis of photosynthetic proteins. The synergistic effect of light and heat stress on photoinhibition is manifested even at relatively "low" PAR and severely under the whole light spectrum after 48 h at 19 °C. At moderate heat stress, the loss of photosynthetic activity is partly due to the inhibition of the acceptor side of the PSII and lower rate of electron transport in chloroplast. The PAR treatment we used at 22 μmol photons m^{-2} s^{-1} is, however, already saturating for the zoospores. At severe heat stress, the inactivation of PSII gradually becomes irreversible, predominantly at the expense of the charge separation in reaction centers of the PSII, dissociation of some specific proteins in the core complex, significant reduction of electron transport rates due to structural rearrangements in thylakoid membranes and disturbances in the system responsible for CO_2 assimilation.[58]

A relatively higher input of short wave irradiation to PAR (high UVR : PAR ratio) was applied in the laboratory. Despite this experimental limitation in simulating the PAR/UV ratios as in the field (which would require a very difficult technical setup), the UV irradiances comparable to those encountered in the field had a negative impact on the photobiology and photochemistry of zoospores of different kelp species. UVR can, however, not be regarded as an "excessive energy input" in a proper sense. Its maximal irradiance is much smaller than of PAR and the UV wavebands do not contribute a significant energy supply for photosynthetic chemistry. Consequently, photoinhibition of photosynthesis was significantly lower under UV-only treatment compared to PAR + UV-A (PA) and PAR + UV-A + UV-B (PAB) treatment among tropical macrophytes exposed to ambient solar radiation.[59] Initiation of photosynthetic recovery processes in some eulittoral macroalgae and seagrass in the presence of low irradiance of short UV-wavelengths was observed. This phenomenon suggests a "positive" UV-B effect which remains controversial and needs further study. This mechanism presents some ecophysiological advantage compared to species which initiate the photosynthetic recovery process during low light or in the absence of UV.[59] Likewise, kinetic study on the PSII damage and repair in the diatom *Thalassiosira pseudonana* showed that the species was able to acclimate to UVR and photosynthetic recovery was already initiated under UVR exposure.[28]

Generally, UV has a direct adverse effect on photosynthesis. The UV-B inhibition spectrum corresponds much more with the spectral absorption by DNA and proteins rather than with photosynthetic pigments.[60] UVR can additionally depress photosynthetic performance by possible damage to the oxidizing site and reaction center of PSII.[61,62] UV-A damage PSII by decreasing electron flow from the reaction centers to plastoquinone[61] affecting electron transport both at the water oxidizing complex and the binding site of the Q_B quinone electron acceptor[62] while UV-B is responsible for the degradation of parts of the D1/D2 heterodimer, the major structural complex within PSII.[63]

Consequently, numerous studies have shown that recovery from photoinhibition is delayed after exposure to additional UV-B irradiation.[22,64] Kelp zoospores have a transitory planktonic phase. Considering their small size and the viscosity of water,[65] they may be able to vertically swim at a speed of 120 μm s^{-1} covering a distance of 1 m in 2 h.[22] Therefore, zoospores released from a 2–4 m tall kelp sporophyte should be able to touch-down and settle into a low-light environment under algal canopies within 8 h. Propagules are also released as a plume of spore cloud. Zoospores with phlorotannin-containing physodes could effectively buffer each other acting as a UV-biofilter.[66] Even with extended exposure of Arctic *A. esculenta* and *L. digitata* zoospores to 24 h of polar day ambient solar radiation at different depths in Kongsfjorden, zoospores were to some extent able to resume their physiological functions and germinate under low PAR in the laboratory.[67]

The ameliorating effects of increased temperature under UVR in Arctic kelp zoospores was observed on the repair of PSII function, showing significantly higher photosynthetic recovery between 7–13 °C compared to 2 °C temperature (Fig. 4d–f). This finding is consistent with the ameliorating effect of moderate temperature increase on the net biological UVR effect reported on photosynthesis and growth of different phytoplankton species[25–28] and in the relatively higher germination capacity of UVR-exposed *Alaria marginata* zoospores at 15 °C compared to 10 °C.[32]

Non-photochemical dissipation of excess light energy is a short-term response, first-line defence and one of the most efficient protective mechanisms against photostress.[68,69] Consequently, during 8 and 48 h measurements, we observed no consistent relationship between combined light and thermal stress and changes in light energy dissipation *via* a non-photochemical pathway; a similar response was observed in high- and low-light acclimated dinoflagellates subjected to thermal stress.[70] Aside from inducing NPQ, other protective mechanisms of the photosynthetic apparatus operating against photooxidation includes: (1) dissipation of light energy in the light-harvesting complex of PSII and low efficiency of its transfer to the core-complex of the PSII, (2) dissipation of excess light energy *via* the proton gradient on the thylakoid membrane, (3) quenching of free radicals in the course of oxidative stress, (4) repair and resynthesis of targets (*e.g.* D1 protein) photodamaged by oxidative stress, (5) changes in the lipid composition of the thylakoid membrane, (6) cyclic electron transport *via* PSII and PSI, (7) aggregation of thylakoid proteins and (8) photorespiration among others.[58]

The temperature optima for photosynthesis in different kelp species' zoospores were observed between 7 °C and 13 °C higher than that of the reported optimum temperature for germination between 2 °C and 12 °C.[33] The same discrepancy between the thermal relationships of growth and photosynthesis in *S. latissima* sporophytes was observed and discussed by Davison.[23,42] The thermal stability of PSII effectively determines the upper temperature tolerance of photosynthesis. Above the temperature optima, the lability of PSII is dependent on the period of heat stress. After 48 h, the germlings were capable of photosynthetic recovery but eventually succumbed to severe temperature stress after 6 days when mortality rate was 100%[33] even in the relatively heat-stress tolerant *A. esculenta.*

Conclusion

In summary, short-term response to increase temperature was non-lethal for Arctic kelp zoospores and can be reversible while a moderate temperature increase had an ameliorating effect on the overall biological effect of UVR. Synergistic effects of environmental stress factors showed different short- and long-term effects and the physiological response was species-specific. Beyond a tolerance breadth, certain algae, *e.g.* Arctic *S. latissima* ecotype (and also the Arctic endemic *L. solidungula*) may be more susceptible to the negative impact of global climate change-related stress factors. The investigated kelp species may be able to survive the projected 6 °C temperature increase in their Arctic habitat but the southernmost distribution range of the species may shift to higher latitude, although natural selection in the southern population exposed to climate change-related stress factors favoring new genotypes is not improbable. The ability for complex metabolic regulation to optimize photosynthesis over the wide range of temperatures and irradiance levels encountered in nature is therefore necessary for the biogeographic distribution extent and limit of a species.

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