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Effects of kelp canopy on underwater light climate and viability of brown algal spores in Kongsfjorden (Spitsbergen)

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Abstract

Spores represent the most vulnerable life history stage of kelps. While UV-induced inhibition of spore germination has been readily documented, the impact of in situ underwater radiation below kelp canopies has been largely overlooked. We determined spectral composition and intensity of underwater radiation along a density gradient in an *Alaria esculenta* kelp forest at 3 m depth in Kongsfjorden, Svalbard. Accordingly, we set up a laboratory experiment simulating five different radiation conditions corresponding to irradiances under very dense to no canopy cover on a cloudless summer day. Spore responses (photosynthetic quantum yield, pigment and phlorotannin contents, swimming activity, and germination success) were determined after 4, 8, 16, and 24 h of exposure. In situ spectral radiation composition differed strongly from conditions applied in previous studies, which underestimated photosynthetically active radiation and overestimated UV-radiation effects. Furthermore, spore solutions differed significantly in quantum yield, pigment, and phlorotannin contents upon release. Nevertheless, spores reacted dynamically to different radiation conditions and exposure times. Highest radiation (PAR 61.8 W m^{-2}, 1.9 W m^{-2} UVA, 0.01 W m^{-2} UVB) caused photodamage after exposure for ≥ 8 h, while intermediate radiation led to photoinhibition. Lowest radiation (PAR 0.23 W m^{-2}, 0 W m^{-2} UVA, 0 W m^{-2} UVB) caused inconsistent reactions. There was a reduction of absolute pigment content in all treatments, but reduction rates of photosynthetic pigments were significantly different between radiation treatments. Soluble phlorotannin content decreased under all conditions but was not significantly affected by experimental conditions. High radiation reduced swimming activity of spores, but experimental conditions had almost no effect on germination success. Consequently, it seems unlikely that in situ radiation conditions negatively affect spores in present and future radiation scenarios.

Keywords UV-radiation · Arctic · *Laminariales* · Photosynthetically active radiation · Germination

Introduction

Climate change will affect polar environments faster and more severely than other regions on earth (Mann et al. 1998; Tokinaga and Xie 2011; Larsen et al. 2014). During the recent years, a severe sea-ice retreat has been observed in the Arctic due to increasing temperatures, and a nearly sea-ice-free Arctic may be expected by 2037 (Wang and Overland 2009). An earlier and prolonged sea-ice-free period might have strong implications for the Arctic marine flora and fauna due to a prolonged exposure to solar radiation (Larsen et al. 2014). In 2011, the first record of ozone depletion comparable to Antarctic ozone loss was detected over the Arctic (Manney et al. 2011), and it is likely that such conditions may occur more often in future (Dameris et al. 2014). Therefore, it is plausible to assume that organisms will have to cope with higher UV-radiation (UVR) throughout longer sea-ice-free seasons.

Kelp forests provide invaluable ecosystem services to coastal temperate and Arctic environments (see, e.g. Christie et al. 2003), but diverse negative impacts of enhanced UVR on kelp spores have been reported by Wiencke et al. (2000), Wiencke et al. (2004), Roleda et al. (2006a, b), Wiencke et al. (2007a), Steinhoff et al. (2008), Müller et al. (2008, 2009), Fredersdorff et al. (2009). These range from direct

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effects on physiological parameters such as photosynthetic quantum yield to integrated parameters such as germination success, making spores the most vulnerable life history stages of kelps (Roleda et al. 2006c). Hence, the former authors concluded that declining ozone concentrations and concomitant higher UVR exposure could negatively affect recruitment in Arctic kelp forests. Most of these studies were performed under laboratory conditions or just below the water surface. Already Wiencke et al. (2006) pointed out that artificial and natural irradiance conditions differ strongly in intensity as well as spectral composition, challenging the transferability of experimental findings to natural ecosystems. Furthermore, the protection of kelp spores from harmful UVR doses by parental canopies is unknown. Pearse and Hines (1979), Gerard (1984), Santelices and Ojeda (1984a, b) and Pavlov et al. (2019) described the strong decrease of incoming radiation though kelp canopies.

In this study, we thus aimed at quantifying the protection of spores by a parental canopy for the first time. We investigated the capability of spores of an Arctic kelp species (*Alaria esculenta*) to biochemically acclimate to radiation conditions mimicking different kelp canopy densities. We simulated the radiation regime in the laboratory according to in situ radiation measurements and quantified physiological responses (photosynthetic quantum yield), biochemical acclimation (phlorotannin and pigment adjustments), as well as germination success of *A. esculenta* spores after exposure to the respective experimental conditions. We hypothesized that parental kelp canopies alter the incoming radiation sufficiently to provide shelter from harmful (excessive) UVR and high photosynthetically active radiation (PAR) for spores within the kelp forest to ensure recruitment.

Material and methods

Alaria esculenta (Linnaeus) Greville dominates the sublittoral zone of Kongsfjorden (79°N, 12°E) below 2.5 m down to 15 m depth together with the kelps *Saccharina latissima*, *Laminaria digitata*, *Saccorhizadermatodea* and *Laminaria solidungula* (Hop et al. 2002; Bartsch et al. 2016).

Preliminary light regime measurements

Solar radiation was measured in-air on the coast of Kongsfjorden on June 16, 2015 at noon and under clear sky conditions with a TriOS RAMSES spectroradiometer (TriOS RAMSES, type SAM ACC UV/VIS; TriOS GmbH, Rastede, Germany; software msda_xe version 7.0; cosine sensor; spectrum from 280 to 700 nm wavelength; calibrated for in-air measurements). These measurements provided the basis for laboratory simulations of high radiation conditions simulating clear days. To determine the underwater radiation regime, the same measuring device (calibrated for underwater measurements) consecutively was placed outside and inside a *A. esculenta* dominated kelp forest at 3 m depth by SCUBA divers on June 17, 2015 under homogenously cloudy conditions off Hansneset, Kongsfjord (N 78°59′05.6″, E 011°57′48.7″, Fig. 1). The sensor was kept vertically. Simultaneously, in-air measurements were conducted with a second device as reference for fluctuations in radiation. Radiation was measured under different kelp densities, ranging from no kelp canopy (outside the kelp forest) to a very dense canopy.

To be able to compare field conditions with other studies, vertical attenuation coefficients (K_d) were calculated according to Kirk (2011):

$K_d = \ln\left(Ed_{(z_2)}/Ed_{(z_1)}\right) \cdot \left(z_1 - z_2\right)^{-1}$, with Ed being radiation at depths z_1 (just below the water surface) and z_2 (3 m depth).

Experimental setup

The in situ radiation measurements served as reference to adjust experimental radiation conditions in the laboratory. First, we calculated UVB—(280–320 nm), UVA—(320–400 nm), and PAR—(400–700 nm) specific attenuation from the light spectra measured in situ on June 17, 2015. We then applied these coefficients to the radiation values recorded on June 16, 2015 to simulate underwater irradiance conditions on a sunny day along a gradient of five different kelp canopy densities. Experimental radiation conditions are summarized in Table 1. Reduction of incoming radiation under no canopy (nc), intermediate canopy (ic), and very dense canopy (vdc) were directly measured in situ, while sparse- (sc) and dense-canopy (dc) radiation climates were linearly extrapolated. For detailed information on kelp forest density in Kongsfjorden, see Bartsch et al. (2016).

All radiation climates were simulated in a walk-in climate chamber at 4 °C using adjustable computer-controlled white-light LEDs (SolarStinger SunStrip, Econlux GmbH, Köln, Germany) and UV fluorescent tubes (UVA 340, Q-Panel, Ohio, USA) with cutoff filter foils (Schott-WG 280 and 320, Schott, Mainz, Germany; Ultraphan 295, Digefra GmbH, München, Germany; Folex 320, Folex GmbH, Köln, Germany) and black net gauze. During the setup, we used integrated values for UVB, UVA, and PAR, as calculated by the TriOS RAMSES software msda_xe (version 7.0, underwater

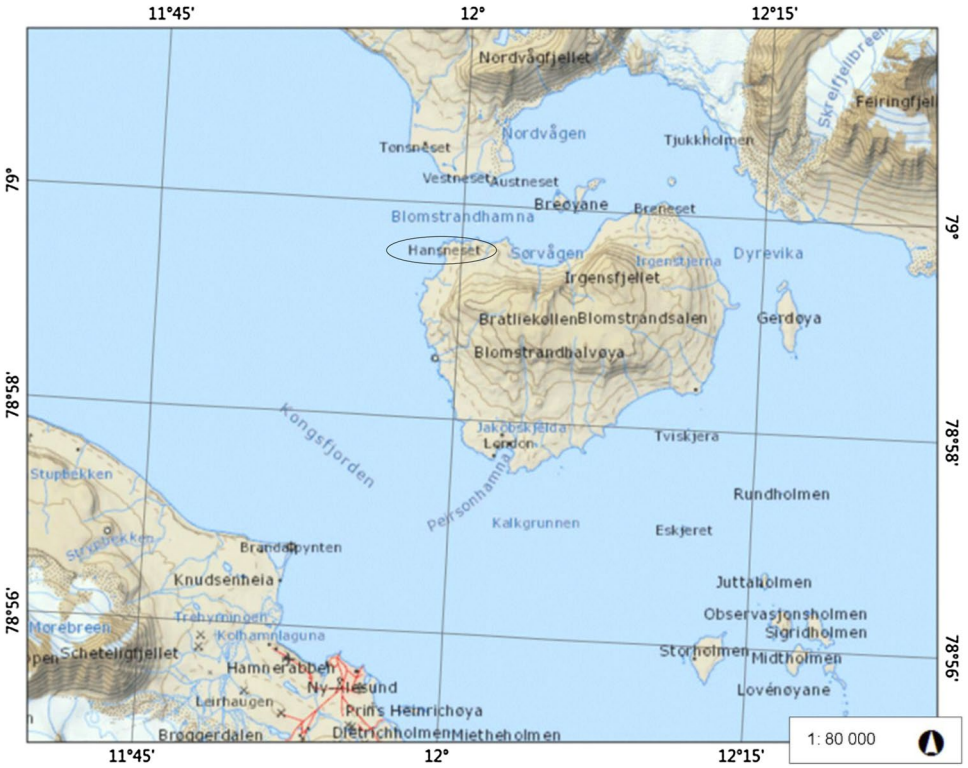

Fig. 1 Study area. All experiments were conducted at the laboratory in Ny-Ålesund. *Alaria esculenta* sporophytes were collected by SCUBA divers off Hansneset. At the same location, the underwater light measurements were conducted. Map © Norwegian Polar Institute (CC BY-NC 4.0)

Table 1 Radiation conditions: Underwater radiation climates as on a sunny day in 3 m depth off Hansneset, Spitsbergen

	Very dense canopy	Dense canopy	Intermediate canopy	Sparse canopy	No canopy
Underwater radiation climates					
PAR (mW m^{-2})	0.25	15.75	31.5	47.25	63
UVA (mW m^{-2})	0	0.375	0.75	1.125	1.5
UVB (mW m^{-2})	0	0.0035	0.007	0.0105	0.014
Experimental radiation climates					
PAR (mW m^{-2})	0.23	14.62	31	45	61.8
UVA (mW m^{-2})	0	0.35	0.68	1.053	1.9
UVB (mW m^{-2})	0	0.0029	0	0.018	0.011

Experimental radiation climates are conditions as applied in the laboratory experiments. To calculate natural underwater radiation climates, attenuation for incoming radiation was measured in situ for UVB, UVA, and PAR under no to very dense kelp canopies. These rates were then applied to in-air radiation measurements on a sunny day to calculate the underwater light regime as under sunny day conditions

calibration) as reference. Calculated and achieved radiation regimes are summarized in Table 1. *Alaria esculenta* spores were then exposed to the different radiation conditions for 4, 8, 16, or 24 h.

Spore release

Fertile specimens of *A. esculenta* were collected by SCUBA divers from 3 m depth off Hansneset and transferred to the laboratory in light-tight barrels filled with fjord water. For the ten consecutive experiments, new specimens were collected weekly from the same site between June 24 and July 18, 2015. The kelps were stored in tanks with running ambient seawater from the fjord under low light conditions. About 40 sporophylls from 10 to 15 randomly selected specimens were mixed to harvest spores not only from single individual sporophytes but to represent the investigated population. For spore release, the sporophylls were processed as follows: After thoroughly wiping the tissue with dishtowels to remove epiphytes, the sporophylls were kept for 24 h in a humid chamber at 4 °C in darkness. Spore release was induced by submerging the sporophylls in temperate (10 °C) filtered seawater (Durapore 0.22 µm Hydrophylic Polyvinylidene Fluoride Membrane Filter, Millipore Corporation

Massachusetts) for 15 min in light on the window board. To calculate spore concentration of the stock solution, a representative subsample was killed with ethanol and counted in a Neubauer "improved" hemocytometer (depth 0.1 mm, smallest grid 0.0025 mm^2, Assistent, Sondheim v. d. Rhön, Germany). To achieve the desired concentrations for the experiments, the stock solutions were diluted with filtered fjord water. Solutions were immediately used in the experiments.

Spore responses

Spore solutions of 1.17×10^6 to 1.78×10^6 spores mL^{-1} were exposed to the five radiation conditions for 4, 8, 16, or 24 h to investigate effects on photosynthetic quantum yield (F_v/F_m), and pigment and phlorotannin contents. Ten consecutive experiments with unique combinations of radiation and exposure time were conducted (Tables 2, 3, alphabetical indices of incubated spore solutions follow the chronological order of the experiments). If not indicated otherwise, all variables were measured in four independent samples, except for post-treatment F_v/F_m which was measured in three independent samples. Each measurement was conducted in triplicate.

For F_v/F_m measurements, 20 mL spore solution was put into 5.4-cm-diameter plastic petri-dishes. Measurements were conducted as triplicates using a Water PAM chlorophyll fluorometer with a WATER-FT flow-through emitter–detector (Walz GmbH, Effeltrich, Germany) at the beginning of the experiment (initial), directly after radiation exposure (treatment effect), as well as 2 h and 24 h after exposure (recovery). Recovery was allowed under dim radiation at 4 °C. For determination of pigment and phlorotannin contents, 40 mL of the spore solution was transferred to 8.5-cm-diameter petri-dishes. Immediately after exposure to experimental conditions, the volume was filtered onto 47-mm-diameter Whatman® GF/C filters, frozen in liquid nitrogen, and stored at − 80 °C until further processing. Initial samples were taken from the diluted stock solution and preserved in the same manner as at the start of the experiment. The deep-frozen samples were transported to the laboratory at the University of Bremen in a precooled dry-shipper.

Pigment and phlorotannin analysis

Prior to extraction and analysis of pigment content, the filters were lyophilized for 24 h. Subsequently, they were cut into narrow strips, put into 2-mL vials and treated as follows. All values were determined as triplicates.

Pigment analysis

Extraction was performed in 2 mL 90% Acetone (Merck, Darmstadt) at 1.5 °C in darkness overnight. Afterward, the samples were centrifuged for 5 min at 13,000 rpm (rcf = 13,792.77) and 4 °C and the solution was filtered through 45 µm nylon syringe filters (Nalgene®, Nalge Nunc International, Rochester, NY, USA). Subsamples of the pigment extract were analyzed in the High-Performance Liquid Chromathography (LaChromElite® with L-2200 autosampler and DAD detector L-2450 by VWR-Hitachi International GmbH, Darmstadt, Germany). For separation of pigments, a Spherisorb® ODS-2 column (25 cm × 4.6 mm, 5-µm particle size; Waters, Milford, MA, USA) with a LiChrosphere® 100-RP-18 guard cartridge was used. Pigment peaks were recorded at 440 nm, and identification and quantification were performed by co-chromatography with standards for Chl *a* and *β*-Carotene (DHI Lab Products, Hørsholm, Denmark) using the software EZChrom Elite ver. 3.1.3. (Agilent Technologies, Santa Clara, CA, USA). Gradients used for identification of pigments were according to Wright et al. (1991). All work steps were performed under dark conditions, and the samples were stored on dry ice between the steps.

Phlorotannin analysis

For phlorotannin analysis, the method described in Cruces et al. (2012) was applied. 2 mL of 70% Acetone (Merck, Darmstadt) was added to the strips, and extraction was conducted by shaking at 0 °C for 24 h in darkness. Afterward, the samples were centrifuged for 10 min at 2500×*g,* and 50 µL of the supernatant was transferred into a new Eppendorf Cup. Immediately, 250 µL dH_2O, 200 µL 20% $NaCO_3$, and 100 µL 2 N Folin-Ciocalteu (Sigma-Aldrich, Steinheim, Germany) were added, and the cups stored for 45 min at room temperature in darkness. After centrifugation for 3 min at 2000 g, 250 µL of the supernatant was transferred to microwell plates for photometric absorbance measurements at 730 nm (FLUOStar OPTIMA; BMG Labtech GmbH; Ortenberg, Germany). A calibration curve was created with Phloroglucinol (Sigma-Aldrich, Seelze, Germany) as standard.

Germination success

Germination success was examined using solutions of 1.17×10^5 to 1.78×10^5 spores mL^{-1}. 20 mL of the solution was transferred to petri-dishes of 5.4 cm diameter with a cover slip placed at the bottom. During and after experimental treatments, spores were allowed to settle and germinate under dim radiation at 4 °C for 3 days. Subsequently, 300 spores were counted on each coverslip with a microscope to calculate the ratio of germinated-to-not-germinated spores. Spores with a germination tube were considered germinated. No differentiation was made between dead and living spores without tube which were both classified as "not-germinated." To distinguish radiation effects from intrinsic

Table 2 Initial and response summaries (F_v/F_m and phlorotannin content): Initial and post-treatment F_v/F_m and phlorotannin measurements for each conducted experiment with results from statistical tests (*t* test or ANOVA, asterisks = significant effects)

Zoospore solution	Density (n mL^{-1})	Experimental conditions		F_v/F_m			Phlorotannins (µg $zoospore^{-1}$)		
		radiation	Exposure time	Initial value	Post-treatment value radiation × time)	Treatment effects	Initial value	Post-treatment value (radiation × time)	Treatment effects
a	1.17×10^6	nc vdc	4	0.378 ± 0.028, $n = 3$	↓ nc × 4: 0.094 ± 0.026, $n = 3$ ↑ vdc × 4: 0.524 ± 0.006, $n = 3$	Radiation: $t2.216 = 27.653$; $p = 0.0007$*	$9.639 \times 10^{-7} \pm 1.436 \times 10^{-7}$, $n = 3$	nc × 4: not measured – 0 × 4: $6.871 \times 10^{-7} \pm 7.473 \times 10^{-8}$, $n = 4$	
b	1.2×10^6	nc vdc	8 24	0.313 ± 0.009, $n = 3$	↓ nc × 8: 0.019 ± 0.002, $n = 3$ ↓ vdc × 8: 0.273 ± 0.009, $n = 3$ ↓ nc × 24: 0.018 ± 0.003, $n = 4$ ↓ vdc × 24: 0.246 ± 0.089, $n = 4$	Radiation × time: ($F(1,10) = 0.114$; $p = 0.742$ Radiation: $F(1,10) = 583.95$; $p = < 0.0001$* Time: $F(1,10) = 0.968$; $p = 0.348$ (2-way ANOVA on log-transformed data)	$4.577 \times 10^{-7} \pm 1.919 \times 10^{-8}$, $n = 3$	↓ nc × 8: $3.727 \times 10^{-7} \pm 4 \times 10^{-8}$, $n = 4$ ↓ vdc × 8: $3.624 \times 10^{-7} \pm 2.367 \times 10^{-8}$, $n = 3$ – nc × 24: $4.103 \times 10^{-7} \pm 1.622 \times 10^{-7}$, $n = 4$ ↓ vdc × 24: $3.501 \times 10^{-7} \pm 3.662 \times 10^{-7}$, $n = 4$	Radiation × Time: $F(1,11) = 2.365$, $p = 0.152$ Radiation: $F(1,11) = 4.998$, $p = 0.047$* Time: $F(1,11) = 0.809$, $p = 0.388$
c	1.17×10^6	nc vdc	16	0.358 ± 0.004, $n = 3$	↓ nc × 16: 0.022 ± 0.002, $n = 3$ ↑ vdc × 16: 0.429 ± 0.017, $n = 3$	Radiation: $t2.031 = 40.244$; $p = 0.0006$*	$9.369 \times 10^{-7} \pm 1.436 \times 10^{-7}$, $n = 3$	– nc × 16: $9.701 \times 10^{-7} \pm 1.701 \times 10^{-7}$, $n = 4$ – vdc × 16: $7.255 \times 10^{-7} \pm 1.249 \times 10^{-7}$, $n = 4$	Radiation: $t4.921 = 0.100$, $p = 0.924$
d	1.78×10^6	sc dc	4 16	0.215 ± 0.004, $n = 4$	↓ sc × 4: 0.022 ± 0.001, $n = 3$ ↓ dc × 4: 0.168 ± 0.02, $n = 3$ ↓ sc × 16: 0.037 ± 0.032, $n = 5$ ↓ dc × 16: 0.073 ± 0.062, $n = 3$	Radiation × time: $F(1,10) = 5.386$; $p = 0.043$* Radiation: $F(1,10) = 35.506$; $p = 0.0001$* Time: $F(1,10) = 3.809$; $p = 0.08$	$1.361 \times 10^{-6} \pm 6.730 \times 10^{-8}$, $n = 4$	↓ sc × 4: $7.83 \times 10^{-7} \pm 2.648 \times 10^{-8}$, $n = 4$ ↓ dc × 4: $8.557 \times 10^{-7} \pm 1.437 \times 10^{-7}$, $n = 4$ ↓ sc × 16: $6.865 \times 10^{-7} \pm 8.503 \times 10^{-8}$, $n = 4$ ↓ dc × 16: $6.973 \times 10^{-7} \pm 8.766 \times 10^{-8}$, $n = 4$	Radiation × Time: $F(1,12) = 0.114$, $p = 0.742$ Radiation: $F(1,12) = 0.013$, $p = 0.914$ Time: $F(1,12) = 5.053$, $p = 0.044$*
e	1.73×10^6	sc dc	8	0.202 ± 0.003, $n = 4$	↓ sc × 8: 0.03 ± 0.02, $n = 3$ ↓ dc × 8: 0.038 ± 0.015, $n = 3$	Radiation: $t3.735 = -0.565$; $p = 0.604$	$1.105 \times 10^{-6} \pm 1.849 \times 10^{-8}$, $n = 3$	↓ sc × 8: $6.887 \times 10^{-7} \pm 3.901 \times 10^{-8}$, $n = 4$ ↓ dc × 8: $7.588 \times 10^{-7} \pm 5.423 \times 10^{-8}$, $n = 4$	Radiation: $t5.449 = -2.098$, $p = 0.085$
f	1.72×10^6	sc dc	24	0.248 ± 0.005, $n = 3$	↓ sc × 24: 0.02 ± 0.002, $n = 3$ ↓ dc × 24: 0.019 ± 0.002, $n = 3$	Radiation: $t4 = 0.802$; $p = 0.468$	$9.790 \times 10^{-7} \pm 2.894 \times 10^{-8}$, $n = 3$	↓ sc × 24: $7.165 \times 10^{-7} \pm 2.539 \times 10^{-8}$, $n = 3$ ↓ dc × 24: $6.375 \times 10^{-7} \pm 7.179 \times 10^{-8}$, $n = 4$	Radiation: $t3.920 = 2.038$, $p = 0.113$
g	1.23×10^6	ic	4	0.233 ± 0.003, $n = 3$	↓ 0.021 ± 0.004, $n = 3$		$1.199 \times 10^{-6} \pm 3.159 \times 10^{-8}$, $n = 3$	↓ $7.482 \times 10^{-7} \pm 2.357 \times 10^{-8}$, $n = 3$	
h	1.76×10^6	ic	8	0.246 ± 0.004, $n = 4$	↓ 0.022 ± 0.002, $n = 3$		$9.729 \times 10^{-7} \pm 3.000 \times 10^{-8}$, $n = 3$	↓ $6.660 \times 10^{-7} \pm 2.364 \times 10^{-8}$, $n = 4$	
i	1.78×10^6	ic	16	0.318 ± 0.003, $n = 3$	↓ 0.022 ± 0.003, $n = 3$		$8.037 \times 10^{-7} \pm 3.958 \times 10^{-8}$, $n = 3$	$-5.785 \times 10^{-7} \pm 2.929 \times 10^{-8}$, $n = 3$	
j	1.34×10^6	ic	24	0.288 ± 0.006, $n = 4$	↓ 0.022 ± 0.004, $n = 3$		$7.433 \times 10^{-7} \pm 6.077 \times 10^{-8}$, $n = 3$	↓ $5.933 \times 10^{-7} \pm 7.046 \times 10^{-7}$, $n = 4$	

Arrows (↓,↑) indicate significant decreases and increases of post-treatment values compared to initial values (= no change)

Mean ± SD, *n* number of replicates, *nc* no canopy, *sc* sparse canopy, *ic* intermediate canopy, *dc* dense canopy, *vdc* very dense canopy

Table 3 Initial and response summaries (pigment contents): Initial and post-treatment Chl *a* and *β*-Carotene contents for each conducted experiment with results from statistical tests (*t* test or ANOVA, asterisks = significant effects)

Zoospore solution	Density (n mL^{-1})	Experimental conditions		Chlorophyll *a* (µg $zoospore^{-1}$)			*β*-Carotene (µg $zoospore^{-1}$)		
		Radiation	Exposure time	Initial value	Post-treatment value radiation × time)	Treatment effects	Initial value	Post-treatment value (radiation × time)	Treatment effects
a	1.17 × 10^6	nc vdc	4	$2.042 \times 10^{-5} \pm 1.261 \times 10^{-6}$, $n = 4$	↓ nc × 4: $1.631 \times 10^{-5} \pm 3.813 \times 10^{-7}$, $n = 4$ ↓ vdc × 4: $1.245 \times 10^{-5} \pm 8.564 \times 10^{-7}$, $n = 4$	Radiation: $t4.144 = -8.251$, $p = 0.001$*	$5.128 \times 10^{-7} \pm 4.274 \times 10^{-8}$, $n = 4$	↓ nc × 4: $2.778 \times 10^{-7} \pm 2.467 \times 10^{-8}$, $n = 4$ ↓ vdc × 4: $1.282 \times 10^{-7} \pm 3.489 \times 10^{-8}$, $n = 4$	Radiation: $t5.4 = -7$, $p = 0.0007$*
b	1.2 × 10^6	nc vdc	8 24	$2.082 \times 10^{-5} \pm 1.684 \times 10^{-7}$, $n = 4$	↓ nc × 8: $1.139 \times 10^{-5} \pm 2.069 \times 10^{-6}$, $n = 4$ ↓ vdc × 8: $8.292 \times 10^{-6} \pm 5.53 \times 10^{-7}$, $n = 4$ ↓ nc × 24: $1.142 \times 10^{-5} \pm 8.933 \times 10^{-7}$, $n = 4$ ↓ vdc × 24: $7.063 \times 10^{-6} \pm 9.515 \times 10^{-7}$, $n = 4$	Radiation × time: $F(1,12) = 1.002$; $p = 0.337$ Radiation: $F(1,12) = 35.336$, $p = < 0.0001$* Time: $F(1,12) = 0.921$; $p = 0.356$	$5.372 \times 10^{-7} \pm 1.2 \times 10^{-8}$, $n = 4$	↓ nc × 8: $2.396 \times 10^{-7} \pm 6.014 \times 10^{-8}$, $n = 4$ ↓ vdc × 8: $1.51 \times 10^{-7} \pm 1.042 \times 10^{-8}$, $n = 4$ ↓ nc × 24: $2.24 \times 10^{-7} \pm 2.621 \times 10^{-8}$, $n = 4$ ↓ vdc × 24: $9.375 \times 10^{-8} \pm 6.477 \times 10^{-8}$, $n = 4$	Radiation × time: $F(1,12) = 0.807$, $p = 0.387$ Radiation: F(1,12) = 22.235, p = 0.0005* Time: $F(1,12) = 2.471$, $p = 0.142$
c	1.17 × 10^6	nc vdc	16	$1.883 \times 10^{-5} \pm 1.877 \times 10^{-6}$, $n = 4$	– nc × 16: $1.781 \times 10^{-5} \pm 1.561 \times 10^{-7}$, $n = 4$ ↓ vdc × 16: $1.157 \times 10^{-5} \pm 1.434 \times 10^{-6}$, $n = 4$	Radiation: $t4.208 = -5.415$, $p = 0.0049$*	$3.561 \times 10^{-7} \pm 4.935 \times 10^{-8}$, $n = 4$	– nc × 16: $3.098 \times 10^{-7} \pm 7.3 \times 10^{-8}$, $n = 4$ ↓ vdc × 16: $1.816 \times 10^{-7} \pm 8.810 \times 10^{-8}$, $n = 4$	Radiation: $t5.799 = -2$ to 241, $p = 0.068$
d	1.78 × 10^6	sc dc	4 16	$4.152 \times 10^{-5} \pm 8.001 \times 10^{-6}$, $n = 4$	– sc × 4: $3.179 \times 10^{-5} \pm 3.295 \times 10^{-7}$, $n = 4$ – dc × 4: $3.199 \times 10^{-5} \pm 9.755 \times 10^{-7}$, $n = 4$ ↓ sc × 16: $2.38 \times 10^{-5} \pm 1.167 \times 10^{-6}$, $n = 4$ ↓ dc × 16: $2.855 \times 10^{-5} \pm 1.574 \times 10^{-6}$, $n = 4$	Radiation × time: $F(1,12) = 16.85$, $p = 0.00146$* Radiation: $F(1,12) = 20$, $p = 0.0008$* Time: $F(1,12) = 106.81$, $p = < 0.0001$*	$1.112 \times 10^{-6} \pm 2.599 \times 10^{-7}$, $n = 4$	– sc × 4: $8.778 \times 10^{-7} \pm 2.689 \times 10^{-8}$, $n = 4$ – dc × 4: $8.708 \times 10^{-7} \pm 6.881 \times 10^{-8}$, $n = 4$ ↓ sc × 16: $6.039 \times 10^{-7} \pm 1.622 \times 10^{-8}$, $n = 4$ ↓ dc × 16: $7.093 \times 10^{-7} \pm 5.317 \times 10^{-8}$, $n = 4$	Radiation × time: $F(1,12) = 5.908$, $p = 0.032$* Radiation: $F(1,12) = 4.523$, $p = 0.055$ Time: $F(1,12) = 88.708$, $p = < 0.0001$*
e	1.73 × 10^6	sc dc	8	$3.906 \times 10^{-5} \pm 1.337 \times 10^{-5}$, $n = 4$	– sc × 8: $2.133 \times 10^{-5} \pm 2.385 \times 10^{-6}$, $n = 4$ – dc × 8: $2.935 \times 10^{-5} \pm 1.935 \pm 10^{-6}$, $n = 4$	Radiation: $t5.756 = 5.219$, $p = 0.002$*	$1.002 \times 10^{-6} \pm 4.424 \times 10^{-7}$, $n = 4$	– sc × 8: $4.697 \times 10^{-7} \pm 1.091 \times 10^{-7}$, $n = 4$ – dc × 8: $7.587 \times 10^{-7} \pm 5.958 \times 10^{-8}$, $n = 4$	Radiation: $t4.643 = -4.650$, $p = 0.007$*
f	1.72 × 10^6	sc dc	24	$2.082 \times 10^{-5} \pm 8.42 \times 10^{-8}$, $n = 4$	↓ sc × 24: $1.142 \times 10^{-5} \pm 8.933 \times 10^{-7}$, $n = 4$ ↓ dc × 24: $1.465 \times 10^{-5} \pm 6.539 \times 10^{-7}$, $n = 4$	Radiation: $t4.360 = -3.508$, $p = 0.021$*	8.14×10^{-7}, $n = 2$	↓ sc × 24: $2.398 \times 10^{-7} \pm 8.350 \times 10^{-8}$, $n = 4$ (↓) dc × 24: $3.416 \times 10^{-7} \pm 1.453 \times 10^{-8}$, $n = 4$	Radiation: $t3.182 = -2.401$, $p = 0.091$
g	1.23 × 10^6	ic	4	4.034×10^{-5}, $n = 2$	– $3.512 \times 10^{-5} \pm 4.333 \times 10^{-6}$, $n = 4$		1.077×10^{-6}, $n = 2$	↓ $8.435 \times 10^{-7} \pm 1.343 \times 10^{-7}$, $n = 4$	
h	1.76 × 10^6	ic	8	$3.348 \times 10^{-5} \pm 8.245 \times 10^{-8}$, $n = 3$	↓ $2.048 \times 10^{-5} \pm 8.913 \times 10^{-7}$, $n = 4$		$8.665 \times 10^{-7} \pm 5.914 \times 10^{-8}$, $n = 4$	↓ $5.043 \times 10^{-7} \pm 2.720 \times 10^{-8}$, $n = 4$	

Table 3 (continued)

Zoospore solution	Density (n mL^{-1})	Experimental conditions		Chlorophyll *a* (µg zoospore^{-1})			*β*-Carotene (µg zoospore^{-1})		
		Radiation	Exposure time	Initial value	Post-treatment value radiation × time)	Treatment effects	Initial value	Post-treatment value (radiation × time)	Treatment effects
i	1.78 × 10^6	ic	16	$3.522 \times 10^{-5} \pm 3.874 \times 10^{-6}$, $n = 4$	↓ $2.180 \times 10^{-5} \pm 1.825 \times 10^{-6}$, $n = 4$		$9.621 \times 10^{-7} \pm 1.285 \times 10^{-7}$, $n = 4$	↓ $5.689 \times 10^{-7} \pm 5.791 \times 10^{-8}$, $n = 4$	
j	1.34 × 10^6	ic	24	$2.532 \times 10^{-5} \pm 3.177 \times 10^{-6}$, $n = 4$	↓ $1.120 \times 10^{-5} \pm 7.135 \times 10^{-6}$, $n = 4$		$5.877 \times 10^{-7} \pm 7.063 \times 10^{-8}$, $n = 4$	↓ $2.612 \times 10^{-7} \pm 1.sc0 \times 10^{-7}$, $n = 4$	

Arrows (↓,↑) indicate significant decreases and increases of post-treatment values compared to initial values (– = no change)

Mean ± SD, *n* number of replicates, *nc* no canopy, *sc* sparse canopy, *ic* intermediate canopy, *dc* dense canopy, *vdc* very dense canopy

effects, a dim radiation control was set up where spores were incubated for 3 days in dim radiation without prior experimental treatment.

Motility of spores

To examine motility of spores over time, suspensions of 8.17×10^6 spores mL^{-1} were transferred to 8.5-cm-diameter petri-dishes and exposed to vdc and nc conditions. Motility was determined upon release as well as after 4, 8, 16, 24, 32, and 48 h of exposure to the respective radiation treatments. To do so, a subsample of the suspension was transferred into a Neubauer "improved" hemocytometer (specifications as above). One line of 1 mm length within the hemocytometer was determined at random for the respective counting session, and for 3 min each, crossing of this line by spores was counted directly in the microscope. If a spore swam in a narrow circle on the line, only one crossing was counted. Results are presented as percent of initial activity.

Statistical analysis

All statistical analyses were performed using the software "R" (version 3.5.2; R Core Team 2018) with the respective packages. Shapiro–Wilk Test for normality (r-core) and Levene Test for homoscedasticity ("car" package: Fox and Weisberg 2011) were performed prior to test statistics. Subsequently, Welch's *t* test or ANOVAs (one-way or two-way according to the respective experimental setup) was applied with radiation and exposure times as independent variables and the respective response parameter as dependent variable. For recovery of F_v/F_m, repeated measure ANOVAs were executed to identify significant recovery effects. As post-hoc test, the Tukey's HSD Test ("agricolae" package: de Mendiburu 2015; "DTK" package for unequal sample sizes: Lau 2013) was executed for identifying significantly different subsample groups. For all analyses, the significance level was set at $\alpha \leq 0.05$. Graphics presented in this text were created with the "Hmisc" package (Harrell 2015) in addition to base graphics. In the following, data are presented as ± standard deviation.

Results

In situ light climate

On June 16, 2015, 165.66 W m^{-2} PAR, 25.31 W m^{-2} UVA, and 0.47 W m^{-2} UVB was measured in-air at noon under clear-sky conditions. At noon of June 17, 2015, in-air radiation measurements was 58.6 ± 5.2 W m^{-2} PAR, 7.8 ± 0.7 W m^{-2} UVA, and 0.3 ± 0.02 W m^{-2} UVB. K_d-coefficients were 1.67 m^{-1} for UVB, 1.42 m^{-1} for UVA, and

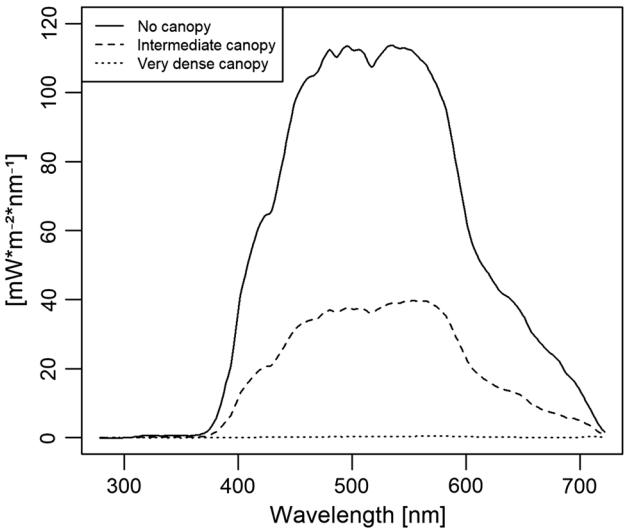

Fig. 2 Underwater light regime. Underwater light climate at 3 m depth on June 17, 2015 under different kelp canopy densities in the Kongsfjord, Svalbard, off Hansneset

0.36 m^{-1} for PAR. Kelp cover strongly reduced the incoming radiation at 3 m depth (Fig. 2). At 3 m depth without kelp canopy, 22.8 W m^{-2} PAR, 0.5 W m^{-2} UVA, and 0.006 W m^{-2} UVB was recorded. Under a very dense kelp canopy, almost no remaining radiation was measured (0.1 W m^{-2} PAR, 0.001 W m^{-2} UVA, and 0 W m^{-2} UVB). Intermediate kelp canopy reduced in-air radiation to 7.7 W m^{-2} PAR, 0.15 W m^{-2} UVA, and 0.002 W m^{-2} UVB.

Response variables

Upon release, spore solutions differed significantly from each other in F_v/F_m values, Chl *a*, *β*-Carotene, and phlorotannin content (Figs. 3, 4 and Tables 2, 3). Because of these significant differences between initial values, responses were examined for each single spore solution and parameter without pooling the results.

Photosynthetic quantum yield

Initial F_v/F_m values ranged from 0.202 ± 0.003 to 0.378 ± 0.028. Significant photoinhibition was observed in all treatments directly after light exposure, except for two vdc simulations (4 and 16 h of exposure; Fig. 3a, Table 2). In general, F_v/F_m showed significant interaction between radiation and exposure time, as well as significant radiation effects. In one experiment, there was a significant interaction effect of exposure time and radiation (solution *d*, sc, vs, dc simulations with 4 and 16 h exposure times). Here, less exposure time under dc conditions led to higher remaining F_v/F_m. Radiation significantly affected F_v/F_m in four experiments with vdc, dc, sc, and nc simulations (solutions *a*–*d*). In all cases, F_v/F_m was significantly lower after exposure to higher radiation. Under nc conditions, reduction of F_v/F_m values varied from 0.3 to 0.094 ± 0.026 ($n = 3$) after 4 h of exposure and to 0.02 after longer exposure times, respectively. After exposure to vdc conditions, the responses were inconsistent: After 4 and 16 h of exposure times, F_v/F_m increased to significantly higher values than the initial ones (4 h: from 0.378 ± 0.028 to 0.524 ± 0.006; 16 h: from 0.358 ± 0.004 to 0.429 ± 0.017; $n = 3$). In contrast, after 8 and 24 h, F_v/F_m was significantly reduced to lower values than the initial one (8 h: from 0.313 ± 0.009 to 0.273 ± 0.009; 24 h: from 0.313 ± 0.009 to 0.246 ± 0.089; $n = 3, 4$). After exposure to nc conditions, full recovery was only apparent in the 4 h experiment (Fig. 3b). After 8 and 24 h, no recovery was observed, while after 16 h, there was a partial recovery of F_v/F_m. In the vdc experiments, the pattern observed directly after light exposure remained the same throughout the recovery time with increased F_v/F_m in the 4 and 16 h experiments and reduced F_v/F_m in the 8 and 24 h experiments (Fig. 3 f).

In experiments with dc and sc conditions, there was a significant interaction effect of radiation and exposure time, with higher radiation and longer exposure times leading to higher reductions in F_v/F_m. In addition, radiation had a significant effect on F_v/F_m. Higher radiation led to significantly stronger decrease in F_v/F_m in one experiment (4 h of exposure, sc conditions: reduction from 0.215 ± 0.004 to 0.022 ± 0.001; dc conditions, $n = 4$: reduction from 0.215 ± 0.004 to 0.168 ± 0.02; $n = 3$). In two experiments (exposure times of 8 and 24 h), no effects were detected. After all treatments with dc or sc conditions, full recovery to initial values was achieved, latest after 24 h. Only spores subjected to sc conditions for 8 h just showed a partial recovery (initial: 0.358 ± 0.006, after treatment: 0.236 ± 0.044). All ic treatments significantly decreased their F_v/F_m values to 0.02, irrespective of initial values. Similar to the sc and dc simulations, full recovery was accomplished in all cases but one (just partial recovery after 24 h in ic conditions; initial value: 0.288 ± 0.006, after treatment: 0.213 ± 0.021, after 24-h recovery: 0.213 ± 0.021).

Pigment contents

Initial Chl *a* contents ranged from $1.9^{-5} \pm 1.9^{-6}$ to $4.5^{-5} \pm 2.0^{-6}$ µg $spore^{-1}$ and initial *β*-Carotene contents from $3.6 \times 10^{-7} \pm 4.9 \times 10^{-8}$ to $1.2 \times 10^{-6} \pm 4.3 \times 10^{-8}$ µg $spore^{-1}$ (Fig. 4a, b, Table 3). Contents of chlorophyll *a* and *β*-Carotene were significantly reduced under most experimental conditions (Chl *a*: $7.063 \times 10^{-6} \pm 9.515 \times 10^{-7}$ to $3.512 \times 10^{-5} \pm 4.333 \times 10^{-6}$; *β*-Carotene: $9.375 \times 10^{-8} \pm 6.477 \times 10^{-8}$ to $8.708 \times 10^{-7} \pm 6.881 \times 10^{-8}$; Table 3). Pigment content did not increase in any of the experiments, and there were not only significant interactions between irradiance and time, but also single factor significances of either

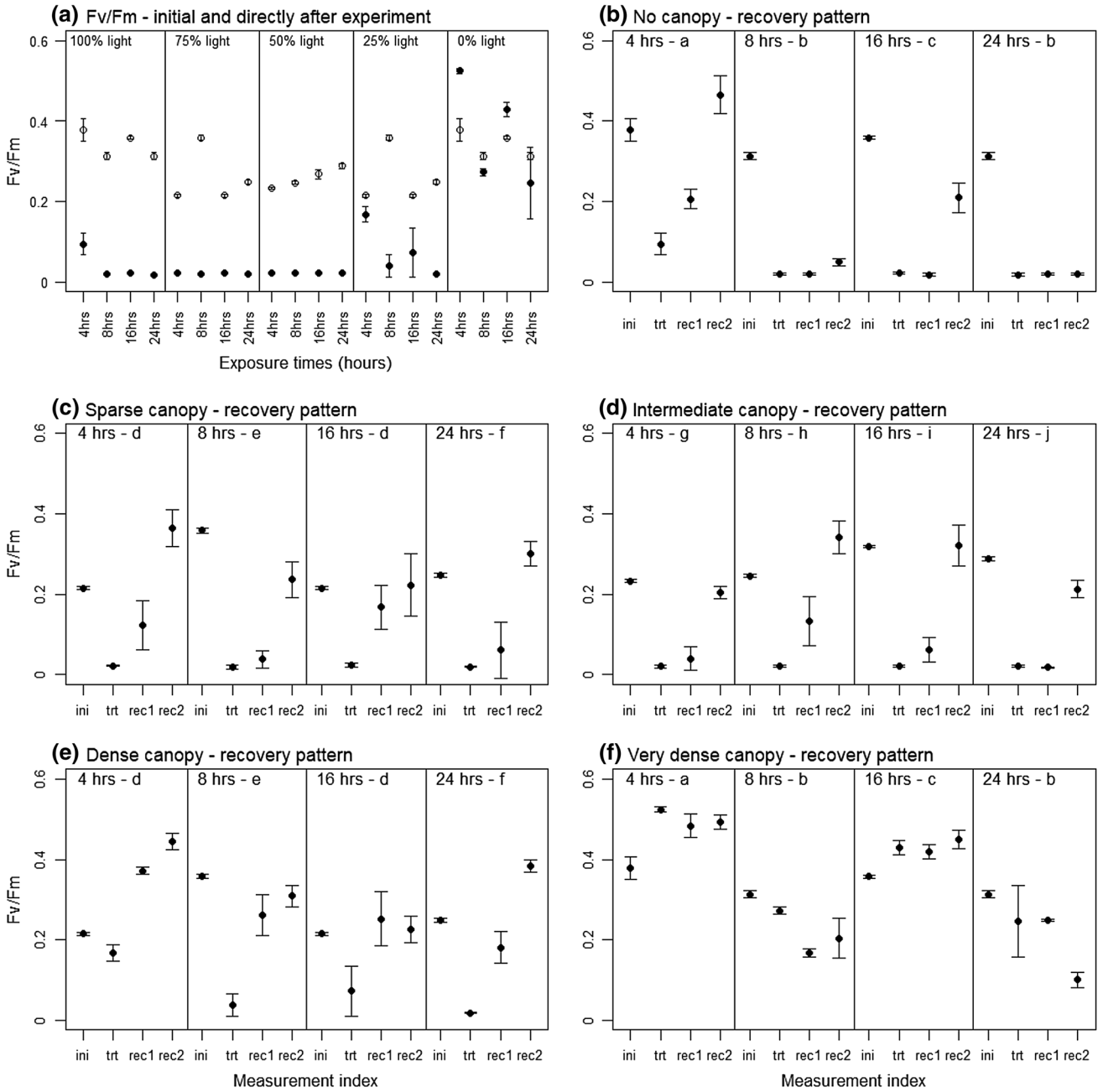

Fig. 3 Summary of F_v/F_m responses (*y*-axis) to respective exposure and recovery times (*x*-axis) and radiation treatments (**b**–**f**). **a** the initial values (open white dots) as well as responses directly after light exposure (black filled dots) for different exposure times. **b**–**f** the initial value (ini), F_v/F_m directly after exposure (trt), as well as after 2 h of recovery (rec1) and 24 h of recovery (rec2) for each light intensity scenario. Exposure times are given in the subpanels. Letters indicate the incubated zoospore solution for easier comparability. All values are mean ± SD. *n* as in Table 2

factor alone among the different experiments. In two experiments (*β*-Carotene, solutions *c* and *f*), the treatment had no significant effect. In general, there were more significant effects for Chl *a* than for *β*-Carotene, with seven significant effects in total for the former and five significant effects for the latter pigment.

In nc and vdc simulation experiments, radiation significantly reduced pigment content. Contents were lower after exposure to vdc conditions than after exposure to nc conditions in both pigments (Table 3—spore solutions *a*–*c*, significant differences after exposure for 4 and 24 h in both pigments). Only in nc simulations for 16 h, contents did not change (Chl *a* initial: $1.883 \times 10^{-5} \pm 1.877 \times 10^{-6}$,

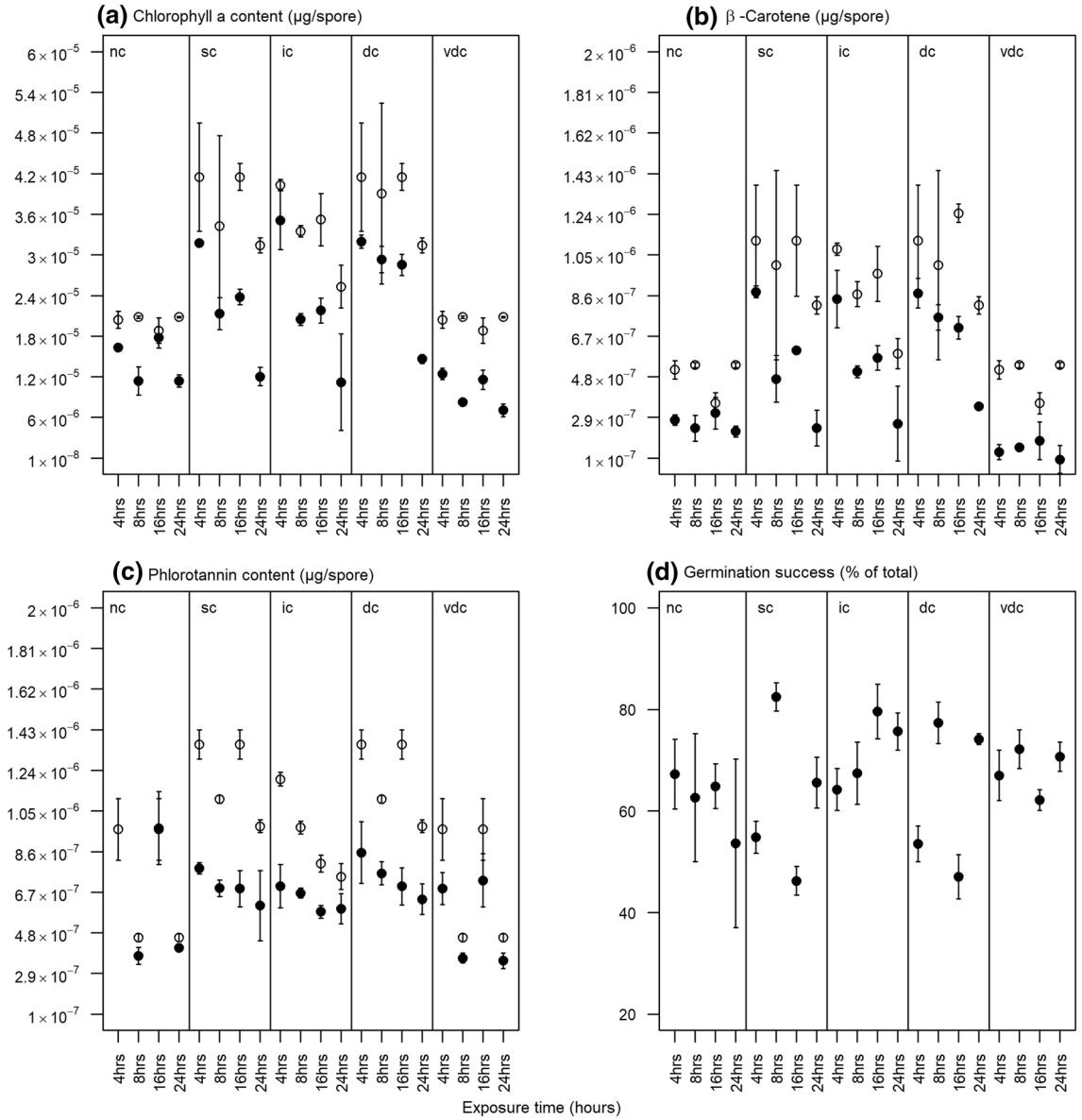

Fig. 4 Zoospore responses to experimental conditions. Initial and post-treatment values of investigated parameters (*y*-axis) after respective exposure times (*x*-axis). Chlorophyll *a* (**a**), *β*-Carotene (**b**) and phlorotannin content (**c**) are given in µg zoospore^{-1}. Germination success (**d**) is given in percent and represents values after the experimental treatment and 3 days of subsequent growth time. White circles are initial values, black filled dots are post-treatment values. Error bars are standard deviation. For exact numbers and number of replicates, refer to Tables 2, 3, and 4. *nc* no canopy, *sc* sparse canopy, *ic* intermediate canopy, *dc* dense canopy, *vdc* very dense canopy

after treatment: nc × 16: $1.781 \times 10^{-5} \pm 1.561 \times 10^{-7}$; *β*-Carotene initial: $3.561 \times 10^{-7} \pm 4.935 \times 10^{-8}$, after treatment: nc × 16: $3.098 \times 10^{-7} \pm 7.3 \times 10^{-8}$). In contrast, in dc and sc simulations, contents were higher after exposure to lower radiation than those after exposure to higher radiation (Table 3—spore solutions *d–f*; significant after 8–24-h exposure in Chl *a* and after 8 and 16 h exposure in *β*-Carotene).

In the dc and sc treatments with 4 and 16 h exposure times (spore solution *d*), there was a significant interaction effect of radiation and exposure times, Chl *a* sc × 4: $3.179 \times 10^{-5} \pm 3.295 \times 10^{-7}$, dc × 4: $3.199 \times 10^{-5} \pm 9.755 \times 10^{-7}$, sc × 16: $2.38 \times 10^{-5} \pm 1.167 \times 10^{-6}$, dc × 16: $2.855 \times 10^{-5} \pm 1.574 \times 10^{-6}$, Radiation × time: $F_{(1,12)} = 16.85$, $p = 0.001$; *β*-Carotene: sc × 4: $8.778 \times 10^{-7} \pm 2.689 \times 10^{-8}$, dc × 4: $8.708 \times 10^{-7} \pm 6.881 \times 10^{-8}$, sc × 16: $6.039 \times 10^{-7} \pm 1.622 \times 10^{-8}$, dc × 16: $7.093 \times 10^{-7} \pm 5.317 \times 10^{-8}$, Radiation × time: $F_{(1,12)} = 5.908$, $p = 0.032$). Higher radiation and longer exposure time led to stronger reduction in pigment content than with either factor alone. In addition, radiation as well as exposure time had significant single effects on the Chl *a*

content (Radiation: $F_{(1,12)} = 20$, $p = 0.0008$; Time: $F_{(1,12)} = 106.81$, $p = < 0.0001$), while for β-Carotene only exposure time had a significant effect (Time: $F_{(1,12)} = 88.708$, $p < 0.0001$). After the 8 and 24 h treatments, pigments were significantly higher after exposure to dc conditions than that after exposure to sc conditions. Only the β-Carotene contents after 24 h did not differ significantly between radiation treatments (Table 3—spore solutions *e*, *f*). Ic conditions for > 8 h led to significant reduction in both pigments compared to initial values (Table 3- spore solutions *g*–*j*).

Phlorotannin content

Initial phlorotannin contents ranged from $4.2 \times 10^{-7} \pm 6.99 \times 10^{-8}$ to $1.4 \times 10^{-6} \pm 6.7 \times 10^{-8}$ µg spore^{-1} (Fig. 4 c). In all experiments, a decrease in phlorotannin content was observed ($3.624 \times 10^{-7} \pm 2.367 \times 10^{-8}$ to $9.701 \times 10^{-7} \pm 1.701 \times 10^{-7}$). Only in the nc treatment with 16 h exposure time, the phlorotannin content stayed constant (initial: $9.369 \times 10^{-7} \pm 1.436 \times 10^{-7}$; after treatment: 9.701 × 10–7 ± 1.701×10^{-7}). In two experiments, radiation or exposure time had a significant effect on the post-treatment values: Exposure to nc conditions led to significantly lower values than exposure to vdc conditions in the 8 versus 24 h exposure time experiment (Table 2—spore solution b, nc × 8: $3.727 \times 10^{-7} \pm 4 \times 10^{-8}$, vdc × 8: $3.624 \times 10^{-7} \pm 2.367 \times 10^{-8}$, nc × 24: $4.103 \times 10^{-7} \pm 1.622 \times 10^{-7}$, vdc × 24: $3.501 \times 10^{-7} \pm 3.662 \times 10^{-7}$; Radiation: $F_{(1,11)} = 4.998$, $p = 0.047$). Exposure time had significant effects in the sc and dc simulations (4 and 16 h experiments), with phlorotannin contents being lower after longer exposure times (spore solution *d*, sc × 4: $7.83 \times 10^{-7} \pm 2.648 \times 10^{-8}$, dc × 4: $8.557 \times 10^{-7} \pm 1.437 \times 10^{-7}$, sc × 16: $6.865 \times 10^{-7} \pm 8.503 \times 10^{-8}$, dc × 16: $6.973 \times 10^{-7} \pm 8.766 \times 10^{-8}$; Time: $F_{(1,12)} = 5.053$, $p = 0.044$).

Germination success

Germination rates in the experiments ranged between 46.3 ± 2.9 and 82.5 ± 2.8% (Table 4, Fig. 4d). Three values from two treatments could not be counted. A dim light control experiment was only conducted once and not for every treatment.

Post-treatment germination rates differed significantly between incubated spore solutions ($F_{(5,56)} = 25.12$, $p < 0.0001$, ranked data) but only in two cases, the experimental treatment had a significant effect on the germination rate: Under dc and sc simulations for 4 and 16 h, spores exposed for longer time had significantly lower germination rates than those after shorter exposure times (spore solution *d*, dc

Table 4 Germination success: Germination success in percent of total incubated zoospores for each conducted experiment with results from statistical tests (*t* test or ANOVA, asterisks = significant effects)

Zoospore solution	Density (n mL^{-1})	Experimental conditions		Germination success (% of total incubated spores)	
		Radiation	Exposure time	Post-treatment value (radiation × time)	Treatment effects
a	1.17×10^5	nc vdc	4	nc × 4: 67.28 ± 6.87, $n = 4$ vdc × 4: 67 ± 4.97, $n = 4$	Radiation: $t5 = 0.059$, $p = 0.955$
b	1.2×10^5	nc vdc	8 24	nc × 8: 62.62 ± 12.61, $n = 4$ vdc × 8: 72.18 ± 3.77, $n = 4$ nc × 24: 53.62 ± 16.56, $n = 4$ vdc × 24: 70.69 ± 2.84, $n = 4$	Radiation × time: F(1, 10) = 4.668, $p = 0.056$ Radiation: F(1, 10) = 0.888, $p = 0.368$ Time: F(1,10) = 0.335, $p = 0.576$
c	1.17×10^5	nc vdc	16	nc × 16: 64.88 ± 4.41, $n = 4$ vdc × 16: 62.18 ± 2.56, $n = 5$	Radiation: t7 = 1.161, $p = 0.284$
d	1.78×10^5	sc dc	4 16	sc × 4: 54.85 ± 3.18, $n = 4$ dc × 4: 53.51 ± 3.52, $n = 4$ sc × 16: 46.26 ± 2.85, $n = 4$ dc × 16: 47.03 ± 4.35, $n = 4$	Radiation × time: F(1,12) = 0.359, $p = 0.56$ Radiation: F(1,12) = 0.026, $p = 0.875$ Time: F(1,12) = 18.326, $p = 0.001$*
e	1.73×10^5	sc dc	8	sc × 8: 82.45 ± 2.78, $n = 4$ dc × 8: 77.36, $n = 4$	Radiation: t6 = 2.073, $p = 0.084$
f	1.72×10^5	sc dc	24	sc × 24: 65.61 ± 4.99, $n = 4$ dc × 24: 74.15 ± 1.07, $n = 4$	Radiation: t3.273 = − 3.348, $p = 0.039$*
g	1.23×10^5	ic	4	ic × 4: 64.24 ± 4.16, $n = 4$	
h	1.76×10^5	ic	8	ic × 8: 67.46 ± 6.12, $n = 4$	
i	1.78×10^5	ic	16	ic × 16: 79.60 ± 5.37, $n = 4$	
j	1.34×10^5	ic	24	ic × 24: 75.65 ± 3.68, $n = 4$	

Arrows (↓,↑) indicate significant decreases and increases of post-treatment values compared to initial values (– = no change)

Mean ± SD, *n* number of replicates, *nc* no canopy, *sc* sparse canopy, *ic* intermediate canopy, *dc* dense canopy, *vdc* very dense canopy

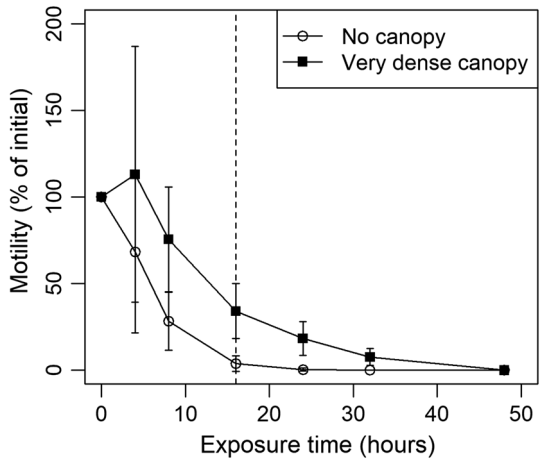

Fig. 5 Radiation effects on zoospore motility. Zoospore motility under no canopy and very dense canopy conditions over time in percent of initial motility. After 16 h, about 20% of the cells exhibited germination tubes in both treatments (dashed line). Mean values ± SD. n=5

and sc conditions for 4 and 16 h: sc × 4: 54.85 ± 3.18%, dc × 4: 53.51 ± 3.52%, sc × 16: 46.26 ± 2.85%, dc × 16: 47.03 ± 4.35%; Time: $F_{(1,12)} = 18.326$, $p = 0.001$). When exposed to the same radiation conditions for 24 h, higher radiation led to significantly lower germination rates (spore solution *f*, dc and sc conditions for 24 h: sc: 65.61 ± 4.99%; dc: 74.15 ± 1.07%; $t3.2725 = 3.3478$, $p = 0.038$). The overall lowest germination rates were measured after 16 h of incubation under dc and sc conditions and the highest germination rate after 8 h of incubation under sc conditions (82.45 ± 2.78%). In the dim light control, 76.9 ± 4.6% of spores germinated within 3 days. Under vdc and nc conditions, there was no significant effect of radiation or time. Responses to ic conditions showed a trend to slightly but insignificantly increasing germination rates with longer exposure times.

Germination success was moderately positively correlated with initial F_v/F_m ($r = 0.49$, $n = 40$, $p = 0.028$; compare initial F_v/F_m and germination success in Figs. 3a and 4d).

Spore motility

There were significant differences in motility over time between vdc and nc simulations with spores under lower radiation exhibiting higher motility over the course of the experiment (Fig. 5). Under nc conditions, a significant reduction in motility was observed after 8 h, and spore motility was almost completely reduced after 16 h of exposure (3.8 ± 4.5% of initial activity). Under vdc conditions, a significant reduction in spore motility was first observed after 16 h, and spore motility was entirely inhibited after 48 h of exposure. After 16 h, germination tubes were observed in approximately 20% of the spores, irrespective of radiation conditions (qualitative observation). These were found neither before nor after this time. After termination of the experiment, spore settlement had taken place under both irradiation conditions, but precise onset of settlement was not evaluated.

Discussion

Light climate

The parental kelp canopy has a tremendous influence on radiation available to understory organisms. This is not limited to quantity but also refers to quality of incoming radiation. Below the densest investigated canopy, radiation was < 1% of the radiation measured outside of the kelp forest at the same depth and UVA and UVB were entirely excluded from the available radiation spectrum. This is even more remarkable as the measured intensities represent values under sunny and clear-sky conditions. Sediment input due to starting ice- and snow-melt may reduce underwater irradiance even more. In Svendsen et al. (2002), average radiation conditions are summarized with maximum irradiances of 170 W m^{-2} (Bischof et al. 1998; Hanelt et al. 2001) or 1300 µmol m^{-2} s^{-1} (Bischof et al. 1999) for PAR and of 19 W m^{-2} for UVA and 1.09 W m^{-2} for UVB (Bischof et al. 1998, 1999) in air. In Hanelt et al. (2001), daily averaged irradiances calculated for the period from March 1 to October 31 during the years 1996–1998 only range from 46.1 to 54.3 W m^{-2} for visible light and from 5.5 to 6.2 W m^{-2} for UVR. On average, only one day of clear sky is observed at Kongsfjorden between June and September (Svendsen et al. 2002). Hence, radiation simulations applied in this study clearly represent rare and extreme radiation conditions. It became evident that natural radiation conditions are very different from experimental conditions applied in previous studies with respect to spectrum composition as well as intensity (Wiencke et al. 2000; Wiencke et al. 2004; Wiencke et al. 2007a; Müller et al. 2008, 2009; Fredersdorff et al. 2009; Steinhoff 2010). In Fig. 6, we summarize the experimental light conditions applied in former studies. Each symbol represents the conditions under which *A. esculenta* spores were incubated in those studies (exposure times of 8 h only). It becomes evident that the focus of previous studies has primarily been laid on UV stress, while PAR intensities have rarely been modified. However, most applied UV intensities were unnaturally high and beyond the limits of usual *in situ* conditions. Wiencke et al. (2006) already noted that in laboratory investigations, PAR was highly underrepresented, whereas UVR was highly overrepresented compared to natural conditions with unknown implications. This has clearly been verified in our study: While natural PAR can be much

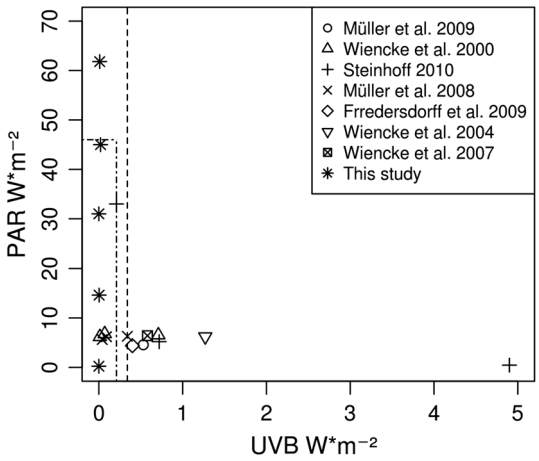

Fig. 6 Thresholds for *Alaria esculenta* zoospore stress responses. Summary of light conditions used in published and this study. Symbols indicate the light conditions applied in the respective studies. Negative effects on zoospore performance are reported for values beyond the dashed and dashed-dotted lines in the respective studies. The UVB threshold for negative effects on germination success is identified at 0.34W m^{-2} (dashed line; unweighted). Negative effects of PAR (> 33W m^{-2}) and UVB (> 0.16W m^{-2}) were observed or reported for values beyond the dashed-dotted lines (unweighted). Negative effects include Fv/Fm reduction without recovery and/or phlorotannin stress responses as reported by the authors of the respective studies. Only results from experiments with exposure times of 8 h are included in this figure.

higher, natural UVR is much lower than that under previously applied experimental conditions.

Freshwater and sediment input strongly affect the underwater radiation regime in Kongsfjorden and particle content can differ by the factor of 17 on very short time scales (Svendsen et al. 2002). Although in our study K_d-values are within the range of previously reported values (see e.g. Svendsen et al. 2002; Wiencke et al. 2006; Pavlov et al. 2019), severe sediment input via melt-water input started after we conducted our measurements, and this led to increased turbidity. Hence, available light in the Kongsfjord will be further decreased throughout the season to much lower values than applied during the experiments in our study. The seasonal decrease of underwater irradiance in situ near our experimental site was also documented recently (Bartsch et al. 2016; Pavlov et al. 2019).

Spore responses

It became evident that spores exhibit a great phenotypic variability upon release. We measured significant differences between initial values in all investigated parameters. These differences did not follow the chronological order of the experiments and low and high values were randomly distributed throughout all treatments. We did not examine effects of preexperimental storage conditions and hence cannot identify a factor which might have influenced the initial conditions. However, sporophytes were held for unequal periods of 0 to 6 days in the storage containers before spore release was induced, which might have led to an acclimation of the collected material to storage conditions as storage conditions were different from conditions at the natural growth site with respect to radiation conditions and biotic influences. Adjustments to light regime (Beale and Appleman 1971; Ramus et al. 1976; Falkowski and LaRoche 1991; Brey 2009), nutrient availability (Aguilera et al. 2002) or season (Wiencke et al. 2007b) are well documented in seaweeds but less well for spores. Furthermore, Wiencke et al. (2007a) suggested that parental adaptations might be mirrored in spores. However, as we did not investigate potential effects of the storage conditions on the spores, we can only speculate about possible influences and thus leave the influence of parental conditions on spores to future studies. In our experiments, spore densities did also differ between incubated solutions. Roleda et al. (2006b) described the UV screening capacity of spore solutions for different kelp species and stated that dense solutions can have a shading effect and protect spores from harmful UVR. However, in Roleda et al.'s (2006b) study, incubated spore solutions were much denser than those in our study, and the differences in density were investigated on a larger scale. In our study, statistical analysis did not identify spore density as a factor with significant effects on the response variables (data not shown). Therefore, the influence of different densities can be neglected in our study when comparing experimental results.

Photophysiological responses

F_v/F_m values were significantly affected by exposure time and radiation conditions. Exposure to 'no canopy' conditions for ≥ 8 h led to permanent photodamage. The spore solutions exposed for 8 and 24 h had the lowest phlorotannin contents of all incubated solutions which could explain higher susceptibility to high radiation. However, only partial recovery was observed with higher phlorotannin content as well (nc conditions for 16 h), leading to the conclusion that high irradiance still has a negative effect on the incubated spores. Samples exposed to reduced radiation showed recovery after photoinhibition to initial values or even above. Wiencke et al. (2000, 2007a) reported reductions in photosynthetic quantum yield after exposure to PAR + UVA and PAR + UVA + UVB. However, in both studies PAR values were just about one tenth of the intensities applied here, while UVA was more than three times higher and UVB more than 50 times higher than in the present study. Therefore, negative radiation effects reported elsewhere might rather be an effect of unnaturally high UVR and will most likely not mirror effects occurring under natural conditions. Decreases in F_v/F_m after exposure to 'very dense canopy' conditions

measured directly after incubation might be a consequence of chlororespiration (Nixon 2000). Clearly, spores are able to cope with naturally occurring irradiances even under highly reduced or no kelp canopies, despite their shade-adaptation (Roleda et al. 2006c). Our simulations suggest that only complete removal of the canopy at the simulated or shallower depth and under sunny conditions will lead to photodamage if experienced for time spans of ≥ 8 h. However, as water transparency and radiation conditions can be reduced enormously by ice and snow melt run-off (see Hop et al. 2002), currents (Svendsen et al. 2002) and weather changes on very short time scales, it is unlikely that spores will experience high irradiances for time spans sufficiently long to cause photodamage.

Pigment contents were significantly influenced by light intensity, exposure time and their interactions, while the phlorotannin contents were only slightly affected by either of these factors. Irrespective of the initial absolute content, samples significantly decreased pigment and phlorotannin contents in almost every investigated scenario. For Chl *a* and *β*-Carotene contents, two different response patterns to radiation and exposure time became apparent. Under 'no canopy' conditions, significantly more pigment content was maintained than that under vdc conditions. This is especially interesting as photodamage was observed after exposure to nc conditions. Therefore, it is likely that spores cannot adapt fast enough to adverse radiation conditions to prevent photodamage. Spores exposed to vdc conditions showed a higher decrease in pigment content compared to nc conditions. Since F_v/F_m decrease was much less pronounced under vdc conditions than that under higher radiation, we conclude that photosynthetic reaction centers are not working at full capacity under these conditions. Hence, it is either not necessary or not possible for the spore to maintain a high pigment content. However, the applied vdc radiation is probably still higher than that under the naturally occurring conditions during most of the summer.

Under 'dense' and 'sparse canopy' conditions, the response pattern in pigment content corresponded to expectations. Here, spores subjected to higher radiation showed a higher decrease in pigment content. As no photodamage was measured under any of these conditions, spores are able to adjust pigment content sufficiently under these conditions. The decrease in pigment content was significantly higher after longer exposure times and evidently there was an excessive amount of pigments per spore in all samples, suggesting that pigment adjustment is a rather slow process over several hours.

Phlorotannin contents were reduced under all experimental conditions. In general, studies on phlorotannins in kelp spores are still scarce. In *A. esculenta*, a decrease in phlorotannin content was observed under high PAR conditions (exposure to 33 ± 19.6 W m^{-2} PAR for 8 h) and similarly in *Saccharina latissima* spores (exposure to 57.2 ± 18.4 W m^{-2} PAR for 8 h), irrespective of additional UVR (Steinhoff 2010). The PAR intensity used in the experiments by Steinhoff (2010) was within the same range as in our study, but the author did not investigate higher or lower PAR intensities. As a conclusion from our study, phlorotannins are not necessarily responding to light conditions, but might be subdued to other drivers. Former studies revealed that a decrease in intracellular phlorotannin content might be the result of soluble phlorotannin exudation (Schoenwaelder and Clayton 1998; Roleda et al. 2005, 2006b; Wiencke et al. 2007a; Steinhoff et al. 2008). This aspect was not investigated here. Furthermore, phlorotannins play a role in cell-wall formation which implies a shift from soluble to cell-wall bound phlorotannins (Schoenwaelder 2002). Analysis of cell-wall bound phlorotannins requires further solubilization steps (Koivikko et al. 2005) and has not been analyzed in this study. Since phlorotannin contents decreased over exposure time (irrespective of initial values), we suggest that this is not a direct response to light conditions, but might rather indicate a shift from soluble to cell-wall bound phlorotannins during spore development (see below). Although phlorotannins seem to act as a protective means against high irradiance (Steinhoff 2010), the role of these substances in UV screening is still under debate. We suggest that in our experiments phlorotannins likely follow developmental cellular adjustments.

Germination success and spore activity

Unfortunately, dim light controls were not available for every treatment and spore solution. Therefore, we do not have data on inherent germination capacity of the individual spore solutions. Still, there was a clear effect of spore origin on germination success. Light conditions did not strongly influence the outcome of our experiments and in every experiment at least ~ 50% of the spores developed germination tubes. Negative effects of UVR and/or high PAR on germination success were reported by Wiencke et al. (2006), Müller et al. (2008), Steinhoff et al. (2008), Steinhoff (2010). However, these investigators used unnatural low PAR and high UVR intensities, which are unlikely to represent field conditions. Seasonal effects on spore reactions might play a role in comparing results from different studies (Wiencke et al. 2000, 2004, 2006). As pointed out by Steinhoff (2010), seasonally varying conditions can cause acclimation and adaptation processes in sporophytes resulting in unequal UVR susceptibilities. Furthermore, Steinhoff (2010) suggested that the maturation stage of parental kelp sporophytes is an important factor influencing spore viability and performance. Hence, although our results suggest that natural radiation conditions do not negatively affect spores, susceptibility might be season dependent. This underlines the importance of studies on parental conditions and their

effect on spore recruitment. We measured a moderate positive correlation between initial F_v/F_m values and germination success, demonstrating that initial spore quality determines germination success of the incubated spore solution.

Motility of spores was clearly influenced by irradiance. Under high radiation conditions, spore motility decreased earlier than that under low radiation conditions. This suggests induction of settlement when light requirements are met, and competition for light with larger individuals is excluded. However, the observed photodamage after constant exposure to nc conditions suggests that spores might also become immobile due to cell-damage under these conditions. In contrast, in both treatments (no canopy and very dense canopy) germination tubes developed 16 h after release irrespective of radiation conditions. Therefore, the onset of germination might be induced by intrinsic rather than extrinsic factors and cessation of motility could be attributed to settlement (see also Pillai et al. 1992; Reed et al. 1992). Tube formation is accompanied by substantial organizational changes within the spores (Pillai et al. 1992). Hence, it is crucial for upcoming studies to further investigate changes in metabolism during the spore's developmental process: It is not clear to what extent these changes are accompanied by internal modifications on a metabolic level, e.g. in enzyme synthesis rate and concomitant repair capacity for photodamage. Therefore, a comparison of responses to environmental conditions over longer time spans might allow observing consecutive developmental stages and elucidate their different response mechanisms to external stressors.

Figure 6 summarizes all available data (published and this study) on thresholds for UVB and PAR, beyond which stress responses are induced. The limit for UVB is at 0.16 W m^{-2}, and for PAR this limit is at 33 W m^{-2}. While PAR intensity at which germination success is inhibited has not been identified so far, UVB of 0.34 W m^{-2} leads to reduced germination success. It becomes evident that highest natural intensities are 25 fold lower than those that negatively affect germination success.

Conclusions and outlook

We clearly demonstrated that laboratory radiation conditions in previous studies were strongly different from natural conditions. The applied intensities differed, and also spectral composition was skewed. Negative effects on spores by high UVR or PAR are unlikely to occur naturally at the investigated site. However, as spore responses differ with sampling season (Wiencke et al. 2000, 2004, 2006, 2007a), results from this study might not be valid for material collected during other seasons of the year.

The parental kelp canopy strongly decreases the available underwater radiation. In addition, times under which protection from high radiation is necessary are probably rare events over the course of the year and not always coinciding with spore release situations. Many kelps in Kongsfjorden are autumn-to-spring fertile (Bartsch, unpublished), thereby avoiding high irradiance situations for their spores, but not *Alaria esculenta* which is summer fertile (Olischläger et al. 2013). Attenuations by the water body and the parental kelp canopy are substantial (this study, Pavlov et al. 2019) and suggest that spores rather have to cope with extremely low radiation rather than with high radiation conditions. PAR and UVR are already buffered through the water body, and hence, even removal of the whole canopy will unlikely lead to irradiation environments impairing recruitment. On a wider geographical scale, this is confirmed by the findings of Krause-Jensen et al. (2007), Krause-Jensen et al. (2012), and Bartsch et al. (2016): Productivity of large brown algae along the Eastern coast of Greenland and in Kongsfjorden is higher under elevated temperatures and prolonged ice-free periods, and many kelps are expected to extend their distributional range northward in future (e.g. Müller et al. 2008; Assis et al. 2016, 2018).

Dynamic adjustments in spore physiology were indicated in pigment content and swimming duration. However, growth conditions of the sporophytes before release and parental investment seem to have great influence on the phenotype and performance of spores. Future studies should investigate parental investment under different environmental and culture conditions to allow for comparison of spore responses to experimental treatments. Metabolic changes and structural reorganization within the short planktonic phase of kelp spores should be investigated to differentiate between internally and externally induced responses.

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Compliance with ethical standards

Conflict of interest The authors have no conflicts of interest to declare regarding this report or study.

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