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Physiological response to irradiance, temperature and co-cultivation in Antarctic engineering brown algae (*Desmarestia menziesii* and *D. anceps*)

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Abstract

The Western Antarctic Peninsula (WAP) is a hot spot of global warming, including decreased sea-ice cover during winter and increased sedimentation during summer due to glacial melt. Subsequently, an altered irradiance and temperature regime in the water column may affect the performance of primary producers and change competitive structures. The brown, subtidal macroalgae *Desmarestia menziesii* and *D. anceps* are ecosystem engineers and of extreme importance for the Antarctic coastal ecosystem. Individuals of both species were collected from the field during the austral summer and exposed in two experiments to different temperatures (2 and 7 °C) or different irradiances (high and low) in combination with co-culturing the two algal species together (two-factorial design). No temperature, irradiance or co-cultivation effects on growth rates of *D. menziesii* and *D. anceps* were detected, but effects were possibly masked by the very low growth rates. Both *D. menziesii* and *D. anceps* are season anticipators, showing highest growth in late winter/spring and a dormancy state during summer. Photosynthetic efficiency was usually higher at 2 °C and low irradiance conditions compared to 7 °C and high irradiance and no co-culturing effects were detected. Parameters derived from P–E curves ($rETR_{max}$, E_k and α) were higher in *D. menziesii* compared to *D. anceps*, reflecting zonation patterns in the field. Future multifactorial experiments, taking seasons and different life-stages into account, are particularly needed to elucidate year-round effects of global warming on macroalgal key species that form the energetic base of the Antarctic coastal food webs.

Keywords Coastal ecosystems · Global climate change · Phaeophyceae · Photosynthesis · Growth · Polar macroalgae · Season anticipators

Introduction

The Western Antarctic Peninsula (WAP) has been described as an area highly vulnerable to the effects of climate change (Clarke et al. 2006; Ducklow et al. 2013; Turley 2013; IPCC 2018). This region is experiencing one of the fastest warming rates in the world (Turner et al. 2009), with a rise in atmospheric temperature of nearly 3 °C since 1951 (Meredith and King 2005), although slowing down in recent years (Turner et al. 2016). At Potter Cove (King George Island/ Isla 25 de Mayo, WAP) average water temperatures increased by 0.32 °C per decade and winter sea surface temperature by more than 2 °C between 1991 and 2006 (Schloss et al. 2012). This increase in water temperature may have profound consequences for shallow polar marine ecosystems, which consist of strongly cold-water-adapted organisms (Clark et al. 2013). Furthermore, high-latitude areas

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suffer from sea-ice loss and retreating glaciers (Cook et al. 2005; Quartino et al. 2013), leading to an increased sediment inflow during the melting season (spring to summer). The consequent reduced light penetration into the water column may affect primary producers along the coastline (Quartino et al. 2013; Deregibus et al. 2016).

Seaweeds are very important primary producers in polar coastal ecosystems, building highly complex underwater forests in the sublittoral rocky shores of the WAP (Wiencke et al. 2014). These seaweed communities play a key role in the Antarctic coastal system, similar to Laminariales (kelp) communities that colonise temperate to Polar rocky coasts of the Atlantic and Pacific Ocean (Clayton 1994). Due to the very low phytoplankton biomass and productivity in some Antarctic shallow coasts, such as Potter Cove—our study area (Hapter et al. 1983; Schloss et al. 1997, 1998, 2002a), seaweeds may be a much more important—year round—carbon source for the Antarctic benthos than in temperate seas (Reichardt 1987). At Potter Cove seaweeds were identified as the main energy source for all consumers and detritivores, forming the energetic base of Potter Cove food web (Marina et al. 2018; Cordone et al. 2018). The order Desmarestiales (Phaeophyceae) represents the dominant taxonomic group within the seaweed community, whose canopy can reach up to 80% of the total macroalgal biomass (Amsler et al. 1995; Quartino and Boraso de Zaixso 2008). Species of this order provide a three-dimensional habitat and a physical shelter for a large number of invertebrates, such as amphipods, epi- and endophytes, and other associated organisms (Amsler et al. 1995; Carlsen et al. 2007; Huang et al. 2007; Bartsch et al. 2008; Barrera-Oro et al. 2018). The perennial Antarctic endemic *Desmarestia menziesii* J. Agardh and *Desmarestia anceps* Montagne form the highest macroalgal biomass in Antarctic coastal areas (together with *Himantothallus grandifolius*; Amsler et al. 1995; Brouwer 1996). Quartino and Boraso de Zaixso (2008) and Gómez et al. (2009) showed that they may reach maxima of up to 10 kg fresh weight m^{-2} at some sites. *Desmarestia menziesii* is a circum-Antarctic species occurring between the Ross Seas and South Georgia Islands, whereas growth of *D. anceps* is mainly restricted to areas around the WAP (Wiencke et al. 2014). Generally, the zonation pattern of the large brown algae is relatively consistent over various sites in Antarctica. While *D. menziesii* dominates the shallow sublittoral zone between 3 and 5 m, *D. anceps* is dominant around 10 m water depths. Both species may co-occur at all depths (Quartino et al. 2001; Wiencke et al. 2014), however, at some sites, only one of these species is present (Wiencke et al. 2014). The vertical depth and biogeographical distribution of macroalgae is mainly controlled by the individual irradiance and temperature requirements of each species (Bartsch et al. 2008; Karsten et al. 2009; Bartsch et al. 2012). Species develop morpho-functional traits that allow them to cope with a determinate depth and latitude (Gómez et al. 2019). Therefore, it is likely that global change will impact the distribution, performance and survival of seaweeds as it alters both temperature regime and irradiance in the water column. Other abiotic factors influencing macroalgal vertical distribution include wave exposure, substrate type and bottom topography (Klöser et al. 1996) as well as other still unknown factors which may shape the local algal distributions (Wiencke et al. 2014).

Besides the regulatory role of abiotic factors, interspecific competition is often considered the major selective force in algal communities determining diversity, species distribution and the biomass and structure of algal communities (Nabivailo and Titlyanov 2006; Barner et al. 2016; Traiger and Konar 2017). Few studies have investigated interspecific relationships among benthic seaweeds occupying the same niche (Reed 1990; Xu et al. 2013; Nabivailo et al. 2014; Chen et al. 2015; Barner et al. 2016), particularly at high latitudes (but see Zacher et al. 2016). Little information is available on the interplay between abiotic and biotic conditions, which is fundamental in order to understand the succession of seaweed communities (Nabivailo et al. 2014; Barner et al. 2016). Interspecific competition may result from "resource" and "interference competition". While resource competition is considered to occur mainly for space, light and nutrients (Bartsch et al. 2008), interference competition is a consequence of chemical interactions between species, influencing the performance of competitors via allelopathy (Olson and Lubchenco 1990).

Previous investigations indicated the lack of multifactorial experiments (Wiencke et al. 2006) and the need to work with field material (Zacher et al. 2016) when evaluating the fate of unique polar ecosystems. Although temperature alone is not likely to endanger the performance of important Antarctic seaweeds (Müller et al. 2009), interaction with other factors such as irradiance and co-cultivation with other species may modify algal responses. Because of their natural zonation and geographical distribution, we hypothesise that *D. menziesii* can better cope with higher irradiance and temperature than *D. anceps* as it is occurring further north and in shallower water depth than the latter. Due to this reason, *D. menziesii* may have an advantage over *D. anceps* in the co-cultivation treatments under high-light and high-temperature conditions, possibly overgrowing *D. anceps* due to a better physiological adaptation. The major aim of this study was to investigate the effect of temperature or irradiance in combination with co-cultivation on the growth and photosynthetic performance of the two Antarctic macroalgae *D. menziesii* and *D. anceps* during their sporophytic life stage, under short-term exposure (approx. 2 weeks).

Material and methods

Sampling site and algal material

Experiments were carried out at the German-Argentinean Dallmann Laboratory, Carlini Station (Potter Cove) between

January and March 2016. An overview of the abiotic and biotic conditions of the Potter Cove ecosystem is given in, e.g., Schloss et al. (2002b) and Deregibus et al. (2016). All algal material was collected from Area A1 ("Peñón de Pesca", 62°23′S, 58°72′W; maps available in Deregibus et al. 2015) 1 to 2 days prior to the experiments, from 5 m depth by scuba divers. Adult sporophytes of the Phaeophyceae *Desmarestia menziesii* and *D. anceps* were collected with the holdfast and brought to the laboratory in dark boxes filled with seawater in order to avoid light stress during transport. Prior to the start of experiments, epiphytes were removed and individuals were kept in constantly aerated seawater containers, separated by species, under low irradiance conditions (~ 10 µmol m^{-2} s^{-1}) at 3 ± 1 °C. A day:night cycle of 16:8 h was applied prior and during each experiment to mimic local long-day conditions. Filtered seawater was exchanged daily. Experiments were conducted with the apical tips of both *Desmarestia* species (10–20 cm, cut around 1 h prior to the start of the acclimation phase).

Experimental design

Two experiments were carried out in a two-factorial design in order to assess the effects of temperature or irradiance on the different species and if these abiotic factors could alter possible competitive effects between the algae (Fig. 1). During the first experiment, the effect of (a) irradiance intensity (low, LL = 10 µmol m^{-2} s^{-1} vs. high, HL = 100 µmol m^{-2} s^{-1}) and (b) culture treatment was tested over a period of 16 days. *Desmarestia menziesii* and *D. anceps* were both grown in mono- and in co-culture with the other species ($n = 5$). Temperature was set to 2 °C. During the second experiment, the effect of (a) temperature (2 °C = ambient summer temperature vs. 7 °C = global warming scenario) and (b) culture treatment was tested over a period of 11 days. As in the first experiment, *D. menziesii* and *D. anceps* were both grown in mono- and in co-culture ($n = 5$). Irradiance was set to 50 µmol m^{-2} s^{-1} (Fig. 1).

Each replicate of a given treatment consisted of two sporophytes, which were grown in aerated 2-L plastic beakers and installed in four water baths controlled by thermostats (Variostat® CC, Huber, Germany). Each treatment consisted of five replicates. In the mono-culture, two sporophytes of the same species were added into each beaker, while in the co-culture one sporophyte of each species was added (Fig. 1). Temperature during each experiment was monitored via data loggers (2.5 ± 0.7 and 7.3 ± 0.3 °C; Hobo Pendant® Temperature/Light Data Logger, USA). The beakers were filled with 0.22 µm filtered seawater (Durapore® Cartridge Filter) with a salinity of 32 PSU (WTW Cond 3150i, Xylem Analytics, Weilheim, Germany). To avoid nutrient depletion and to inhibit diatom growth, seawater was enriched

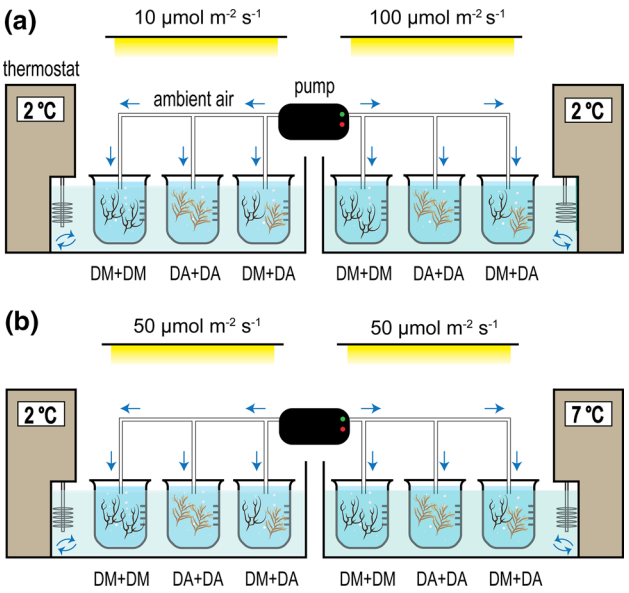

Fig. 1 Experimental design. **a** Experiment 1: Impact of co-cultivation and irradiance intensity on *Desmarestia menziesii* (DM) and *D. anceps* (DA): 10 µmol m^{-2} s^{-1} and 100 µmol m^{-2} s^{-1} were applied to both species mono- (DM, DA) and co-cultured (DM + DA) ($n = 5$) at 2 °C over 16 days with 4 days of acclimation to 10 µmol m^{-2} s^{-1}. **b** Experiment 2: Impact of co-cultivation and temperature on *D. menziesii* and *D. anceps*: 2 °C and 7 °C were applied to both species mono- and co-cultured ($n = 5$); at 50 µmol m^{-2} s^{-1} over 11 days with 3 days of acclimation to the experimental conditions

with nutrients after Provasoli (1968; 50 mL per 10 L of seawater) and with germanium dioxide (0.5 mL of GeO_2 per litre of seawater as described by Shea and Chopin 2007). Media was changed weekly. Light was provided by halogen lamps (NORKA tipo Sirius HIT 150 W, Dörverden-Hülsen, Hamburg, Germany). PAR was measured at the top of each beaker using a flathead LICOR 190 SA quantum sensor (cosine corrected) connected to a LICOR LI-1400 data logger (LICOR, Lincoln, USA). Prior to the start of the experiments, algae were acclimated to the experimental temperatures for 3 to 4 days. The irradiance was set according to field measurements performed on site where approx. 100 photons µmol m^{-2} s^{-1} represents the mean irradiance intensity at 5 m depth during summer, while 50 µmol photons m^{-2} s^{-1} represents the mean irradiance at 10 m depth (Campana et al. 2018). The biomass peak of *D. menziesii* is found at 5 m depth, whereas *D. anceps* has its biomass maximum at 10 m depth (Quartino et al. 2001).

Algal growth and photosynthetic efficiency

Growth rate and photosynthetic parameters were determined to document the effects of temperature, irradiance and co-culturing treatments on macroalgae performance.

Pre-experimental fresh weight (*FW*, mg) was measured when the algal material was transferred into the beakers for acclimation (Day 4 and 3 for experiments 1 and 2, respectively). Subsequently, *FW* was measured when the experiment started or one day earlier (initials), at the midpoint (Day 6 for both experiments) and at the endpoint of the experiment (Day 16 and 11 for experiments 1 and 2, respectively). Before weighing, the sporophytes were carefully blotted one by one with tissue paper (Sartorius CPA323S-0CE, Germany). Overall growth rates from the initial measurements (initials) until the last day of the experiment were calculated as

$$\text{Specific growth rate}\left(\mu, \text{day}^{-1}\right) = 100\frac{\ln N_t N_0^{-1}}{t},$$

where N_0 is the initial FW, N_t is the *FW* on day t, and t is the time period expressed in day (see also Wiencke and tom Dieck 1989).

In order to assess the baseline physiological performance, pre-experimental photosynthetic efficiency (F_v/F_m) of each sporophyte was measured the day the algal material was transferred into the beakers for acclimation. After that, photosynthetic efficiency was measured on Day 0 (= initials), at the midpoint (Day 7 and 5 for experiments 1 and 2, respectively) and at the endpoint of the experiment (Day 15 and 10 for experiments 1 and 2, respectively). In vivo chlorophyll *a* fluorescence of photosystem II (PSII) was determined as the maximum quantum yield of PSII (F_v/F_m) using a modulation fluorometer (PAM 2100, Walz GmbH, Effeltrich, Germany) connected to a PC running PamWin™ software. At each measurement, the fibre optic was placed ~ 1 cm below the apical tip of the sporophyte. After 3 min of dark adaption, a saturating light pulse (0.8 s; 600 ms completely saturating white light pulse) was applied and minimal (F_0) and maximal (F_m) fluorescence were used to calculate the F_v/F_m using the PAM software as

$$F_v/F_m = \left(F_m - F_0\right)/F_m.$$

Three minutes of dark incubation were chosen because no further increase in F_v/F_m was measured in a pilot study after 3-, 5-, 7-, 10- and 15-min dark adaption, demonstrating 3 min to be sufficient to "open" all reactions centres of PSII.

Additionally, rapid light curves were determined (PAM 2100) right after measurements of F_v/F_m at the initial, the midpoint and the endpoint. The effective PSII quantum yield ($\Phi PSII = (F'_m - F_t)/F'_m$) for the illuminated samples was calculated measuring the steady-state fluorescence in light (F_t) and the maximum light-adapted fluorescence yield (F'_m) of each sporophyte during a stepwise increasing actinic light intensity (from 0 to 402 µmol photons m^{-2} s^{-1}, every 20 s). The light intensities applied by the PAM were corrected with a LI-COR LI-250A Light Meter. The effective quantum yield represents a sensitive indicator of photosynthetic performance and, thus, of the health of algae affected by stress exposure. Estimations of the relative electron transport rates of PSII (rETR) were calculated by multiplying the effective quantum yield of PSII with the corresponding light intensity (E_{PAR} = irradiance in the PAR region; 400–700 nm) as follows:

$$r\text{ETR} = \Delta F/F'_m * E_{PAR}.$$

Photosynthesis versus irradiance curves (P–E curves) with rETR as a function of the irradiance intensity (PAR) were fitted after the hyperbolic tangent model (Jassby and Platt 1976). From each curve, the maximum relative electron transport rate ($rETR_{max}$), the electron transport efficiency (α), and the saturation irradiance for electron transport (E_k, calculated as the intercept between α and $rETR_{max}$) were calculated. These parameters show the photosynthetic performance of the algae under the different treatments and may be used to interpret photo-acclimation.

Statistical analysis

Means and standard deviations (SD) were calculated from five independent replicates per treatment ($n = 5$), each of which was the mean of two pseudo-replicates. Normal distribution of data was tested by the Shapiro–Wilk *W* test. One-way or two-way analysis of variance (ANOVA) was conducted on pre-experimental *FW* and F_v/F_m to assess the similarity of the values within each species among the treatments prior to the experiments. Additionally, two-way ANOVA on pre-experimental *FW* and F_v/F_m was also conducted on mono-cultured *D. menziesii* and *D. anceps* to allow further comparison of the two species over time. Two-way analyses of variance with repeated measures (RM-ANOVA) were conducted to identify statistically significant differences of means of F_v/F_m, $rETR_{max}$, α and E_k of *D. anceps* and *D. menziesii* separately and of only mono-cultured species together under irradiance/temperature and co-cultivation treatments (two levels of each between-subjects factor called 'irradiance' or 'temperature' and 'co-cultivation'), considering the Mauchly's sphericity test (three levels of the within-subjects called 'time': initial, midpoint and endpoint; $\alpha = 0.05$). Where Mauchleys test of sphericity was violated (RM-ANOVA; $\varepsilon < 0.75$), a Greenhouse–Geisser (G–G) correction was applied. Homogeneity of variances was tested using Levene's Test. Post hoc multiple means comparisons were performed with a Tukey's honest significance difference (HSD) test. A 5% significance level ($p = 0.05$) was applied in all statistical tests. All statistical analyses were run using the R statistical software R 3.5.0 (R 241 Development Core Team 2018). Graphics were generated with the ggplot2 package (v. 3.1.1).

Results

Experiment 1: impact of irradiance and co-culturing on *Desmarestia menziesii* and *D. anceps*

Measurements of *FW* from pre-experimental material (Day -4) of *D. anceps* showed a similar distributed weight among the different treatments. In contrast, *D. menziesii* had a significantly higher pre-experimental weight at the high irradiance (1.86 ± 0.06 g) compared to the low irradiance treatment (1.79 ± 0.05 g; two-way ANOVA, $F = 7.23$, $p = 0.02$). Both species showed very low overall growth rates—however significantly different from zero (one-sample *t* test, $p = 0.003$ for *D. menziesii* and $p < 0.0001$ for *D. anceps*)—and no significant differences in growth with different irradiance or culture treatments could be detected (Fig. 2a). *FW* data are shown in Online Resources 1.

F_v/F_m values from pre-experimental material (exposed to low irradiance, Day -4) of both species were similar among the different treatments (Table 1). During the experiment, F_v/F_m of both species was significantly higher at low irradiance (10 µmol m^{-2} s^{-1}) compared to the high irradiance treatment (100 µmol m^{-2} s^{-1}) but no significant culture effect was observed throughout the experiments (Tables 1, 2, Fig. 3a). F_v/F_m values dropped over time in the high irradiance treatment (by 10% in *D. menziesii* and 11% in *D. anceps* between Day 0 and 15), but remained constantly high at low irradiances, resulting in a significant time*irradiance interaction for both species (Tables 1, 2, Fig. 3a).

Generally, $rETR_{max}$ and E_k were lower at low irradiances compared to high irradiances in both species, however, not always significant (Tables 1, 2, Fig. 3a). Both $rETR_{max}$ and E_k of *D. menziesii* showed an interactive effect of time*culture (Table 2, Fig. 3a). While both values remained constant in the mono-culture, they increased at the midpoint in the co-culture and decreased at the endpoint (Tables 1, 2, Fig. 3a).

Comparing the photosynthetic performance of *D. menziesii* and *D. anceps* mono-cultured directly, $rETR_{max}$, α and E_k were significantly higher in *D. menziesii* compared to *D. anceps* (by 32, 17 and 21%, respectively) with lower values at low irradiances as described above for the single species effects (Tables 1, 3, Fig. 3a). F_v/F_m values were similar between the two species throughout the experiment and dropped significantly under the high irradiance treatment, while remaining constant under the low irradiance treatment as explained above for the single species effects (Tables 1, 3, Fig. 3a).

Experiment 2: impact of temperature and co-culturing on *Desmarestia menziesii* and *D. anceps*

Measurements of *FW* from pre-experimental material (Day -3) of *D. menziesii* and *D. anceps* showed a similar distributed weight among the different treatments. As in experiment 1, both species showed very low overall growth rates—however significantly different from zero (one-sample *t* test, $p < 0.0001$ for both *D. menziesii* and *D. anceps*)—and no

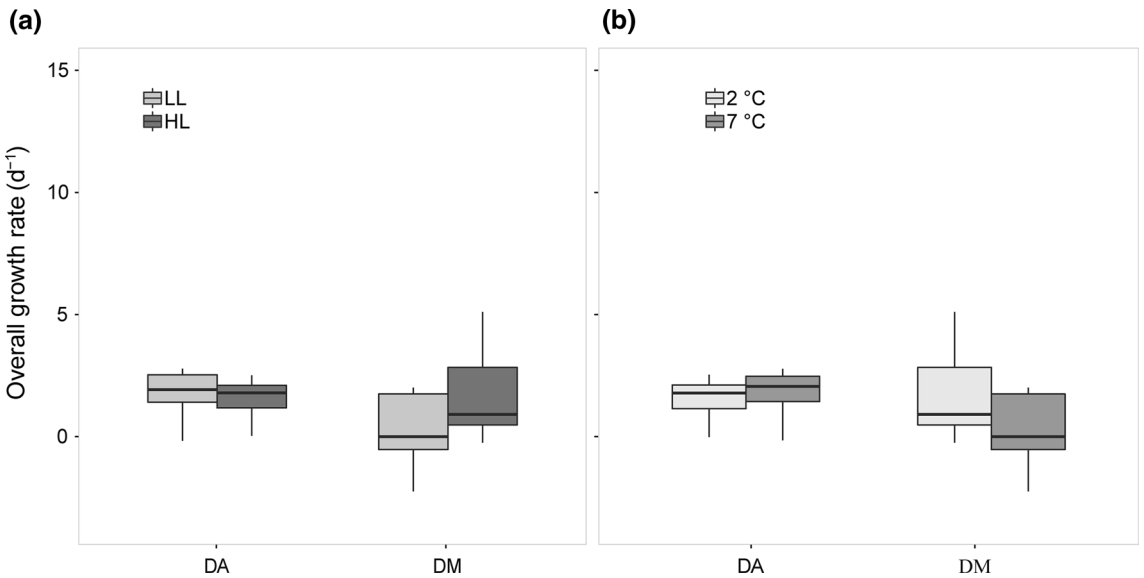

Fig. 2 Experiments 1 (**a**) and 2 (**b**): Box–whisker plots of overall growth rate (Day -1) of *Desmarestia menziesii* (DM) and *D. anceps* (DA), under 10 (LL) and 100 µmol m^{-2} s^{-1} (HL, experiment 1) or at 2 and 7 °C (experiment 2). Experimental duration: 16 days (experiment 1) and 11 days (experiment 2) (median ± 95 to 5 percentile, $n = 5$)

Table 1 F_v/F_m, $rETR_{max}$, α (in µmol m^{-2} s^{-1}) and E_k (in µmol m^{-2} s^{-1}) (mean ± SD) of *Desmarestia menziesii* (DM) and *D. anceps* (DA) before (pre-exp = Day -4 and Day -3) and during the experiment (initial = Day 0, midpoint = Day 7 and 5, endpoint = Day 15 and 10) for experiments (E) 1 and 2, respectively. LL = 10 µmol m^{-2} s^{-1}, HL = 100 µmol m^{-2} s^{-1}

E	Treatment	Species	Pre-exp	Initial				Midpoint			
			F_v/F_m	F_v/F_m	$rETR_{max}$	α	E_k	F_v/F_m	$rETR_{max}$	α	E_k
1	LL mono-culture	DM	0.73 ± 0.02	0.72 ± 0.03	39.4 ± 7.3	0.35 ± 0.05	114.0 ± 16.4	0.71 ± 0.02	44.0 ± 14.9	0.42 ± 0.10	106.2 ± 35.1
		DA	0.73 ± 0.02	0.71 ± 0.02	28.1 ± 10.4	0.34 ± 0.05	82.6 ± 25.6	0.70 ± 0.02	36.3 ± 6.7	0.38 ± 0.05	95.5 ± 6.9
	LL co-culture	DM	0.76 ± 0.02	0.72 ± 0.04	35.6 ± 13.0	0.32 ± 0.08	110.1 ± 17.4	0.69 ± 0.03	52.4 ± 12.1	0.43 ± 0.03	119.9 ± 18.3
		DA	0.75 ± 0.02	0.70 ± 0.04	27.4 ± 13.0	0.38 ± 0.06	74.9 ± 36.9	0.68 ± 0.02	41.6 ± 20.7	0.42 ± 0.07	102.1 ± 50.3
	HL mono-culture	DM	0.73 ± 0.01	0.71 ± 0.03	48.4 ± 3.5	0.39 ± 0.02	126.3 ± 10.8	0.63 ± 0.02	45.2 ± 7.0	0.37 ± 0.04	122.7 ± 9.1
		DA	0.74 ± 0.02	0.66 ± 0.01	36.4 ± 9.8	0.36 ± 0.06	103.1 ± 25.4	0.61 ± 0.05	37.6 ± 15.2	0.33 ± 0.07	108.7 ± 26.5
	HL co-culture	DM	0.72 ± 0.05	0.72 ± 0.03	54.4 ± 7.8	0.40 ± 0.05	136.2 ± 11..0	0.64 ± 0.01	73.0 ± 13.7	0.46 ± 0.07	160.1 ± 12.7
		DA	0.74 ± 0.02	0.69 ± 0.08	31.1 ± 13.5	0.33 ± 0.06	94.2 ± 34.7	0.59 ± 0.06	36.9 ± 10.4	0.32 ± 0.08	116.8 ± 16.2
2	2 °C mono-culture	DM	0.75 ± 0.02	0.73 ± 0.01	60.2 ± 14.7	0.48 ± 0.04	124.0 ± 23.6	0.71 ± 0.02	72.9 ± 14.7	0.51 ± 0.02	142.9 ± 25.1
		DA	0.75 ± 0.02	0.73 ± 0.02	50.0 ± 12.3	0.42 ± 0.05	117.1 ± 21.4	0.70 ± 0.01	55.9 ± 20.4	0.42 ± 0.06	129.4 ± 31.9
	2 °C co-culture	DM	0.75 ± 0.02	0.73 ± 0.03	49.3 ± 17.7	0.43 ± 0.05	114.7 ± 33.7	0.72 ± 0.03	71.6 ± 13.1	0.48 ± 0.03	147.7 ± 19.5
		DA	0.75 ± 0.02	0.72 ± 0.01	45.3 ± 9.5	0.39 ± 0.04	115.0 ± 16.5	0.71 ± 0.02	54.4 ± 10.9	0.43 ± 0.04	125.1 ± 16.0
	7 °C mono-culture	DM	0.75 ± 0.02	0.71 ± 0.01	70.2 ± 16.0	0.48 ± 0.04	146.9 ± 25.1	0.68 ± 0.04	81.1 ± 12.03	0.48 ± 0.06	170.6 ± 9.2
		DA	0.76 ± 0.02	0.71 ± 0.02	34.7 ± 13.4	0.36 ± 0.1	94.5 ± 20.8	0.65 ± 0.03	44.3 ± 3.09	0.38 ± 0.04	117.9 ± 18.5
	7 °C co-culture	DM	0.75 ± 0.02	0.73 ± 0.04	61.4 ± 14.5	0.48 ± 0.06	127.7 ± 19.6	0.69 ± 0.03	76.9 ± 13.3	0.48 ± 0.06	161.2 ± 16.2
		DA	0.76 ± 0.01	0.74 ± 0.02	45.3 ± 9.0	0.42 ± 0.01	108.4 ± 20.0	0.68 ± 0.03	51.8 ± 11.7	0.41 ± 0.072	124.7 ± 12.3

E	Treatment	Species	Pre-exp	Endpoint			
			F_v/F_m	F_v/F_m	$rETR_{max}$	α	E_k
1	LL mono-culture	DM	0.73 ± 0.02	0.73 ± 0.02	43.5 ± 5.7	0.42 ± 0.05	104.9 ± 13.5
		DA	0.73 ± 0.02	0.73 ± 0.02	17.7 ± 3.7	0.26 ± 0.03	67.5 ± 7.4
	LL co-culture	DM	0.76 ± 0.02	0.70 ± 0.02	36.6 ± 11.0	0.39 ± 0.05	96.7 ± 33.8
		DA	0.75 ± 0.02	0.72 ± 0.02	20.4 ± 4.6	0.26 ± 0.07	83.1 ± 24.9
	HL mono-culture	DM	0.73 ± 0.01	0.59 ± 0.07	55.6 ± 12.5	0.42 ± 0.05	131.3 ± 15.3
		DA	0.74 ± 0.02	0.57 ± 0.05	31.0 ± 14.5	0.31 ± 0.04	97.5 ± 35.4
	HL co-culture	DM	0.72 ± 0.05	0.634 ± 0.06	49.7 ± 15.2	0.40 ± 0.07	122.7 ± 19.5
		DA	0.74 ± 0.02	0.56 ± 0.07	24.1 ± 11.7	0.27 ± 0.06	79.9 ± 24.9
2	2 °C mono-culture	DM	0.75 ± 0.02	0.71 ± 0.03	62.7 ± 2.3	0.45 ± 0.03	138.7 ± 8.5
		DA	0.75 ± 0.02	0.70 ± 0.03	53.5 ± 14.2	0.44 ± 0.05	120.2 ± 26.0
	2 °C co-culture	DM	0.75 ± 0.02	0.72 ± 0.01	63.4 ± 15.2	0.47 ± 0.03	134.6 ± 23.3
		DA	0.75 ± 0.02	0.71 ± 0.02	51.8 ± 12.4	0.43 ± 0.06	118.7 ± 17.1
	7 °C mono-culture	DM	0.75 ± 0.02	0.67 ± 0.03	65.4 ± 12.2	0.45 ± 0.06	148.1 ± 31.3
		DA	0.76 ± 0.02	0.65 ± 0.02	40.0 ± 9.5	0.37 ± 0.04	106.8 ± 17.3
	7 °C co-culture	DM	0.75 ± 0.02	0.65 ± 0.03	63.0 ± 14.6	0.45 ± 0.06	139.5 ± 12.6
		DA	0.76 ± 0.01	0.65 ± 0.04	53.5 ± 17.0	0.42 ± 0.08	126.3 ± 22.8

significant differences in growth with different irradiance or culture treatments could be detected (Fig. 2b). *FW* data are shown in Online Resources 1.

F_v/F_m values from pre-experimental material (Day -3) of both species were similar among the different treatments (Table 1). In general, F_v/F_m of both species was higher at 2 °C compared to 7 °C; however, a significant difference was detected for *D. anceps* only (Tables 1, 2; Fig. 3b). Both species showed a significant time*temperature effect on F_v/F_m due to a stronger decrease in F_v/F_m at 7 °C compared to 2 °C over time (Tables 1, 2, Fig. 3b). Similar to the other experiment, no culture effect on F_v/F_m was observed for both species (Table 2).

Almost no significant effect on the other photosynthetic parameters was found for temperature or culture effects, and only $rETR_{max}$ of *D. menziesii* was significantly higher at 7 °C compared to 2 °C (Table 2).

Comparing the photosynthetic performance of *D. menziesii* and *D. anceps* mono-cultured directly, $rETR_{max}$, α and E_k were significantly higher in *D. menziesii* compared to *D. anceps* (by 48, 18 and 27%, respectively), similarly to experiment 1 (Tables 1, 3, Fig. 3b). Both $rETR_{max}$ and E_k were lower at 7 °C compared to 2 °C in *D. anceps*, while it was the other way around for *D. menziesii*, resulting in a species*time interaction (Table 3). F_v/F_m values were similar between the two species throughout the experiment showing a significant time*temperature effect due to a stronger decrease in F_v/F_m at 7 °C compared to 2 °C over time as described above for the single species effects (Tables 1, 3, Fig. 3b).

Discussion

This study investigated whether direct or indirect effects of climate change may alter growth and photosynthetic performance of the two key macroalgal species in Antarctic coastal areas, *D. menziesii* and *D. anceps*. The tested factors were irradiance or temperature (abiotic) and co-culturing (biotic), including the interaction between these factors during short-term exposure (approx. 2 weeks). While no strong effects during co-culturing of the different species combinations were observed, temperature but mostly irradiance led to significant changes in the photosynthetic performance of the species.

Generally, growth of both *Desmarestia* species was too low to detect treatment effects. Wiencke and tom Dieck (1989, 1990) detected optimal growth rates for these species at temperatures ≤ 5 °C, whereas Zacher et al. (2016) could show higher growth rates for *D. anceps* at 5 °C compared to 0 °C in a study with cultured material. Defined as season anticipators (Kain 1989; Wiencke 1990; Gómez and Wiencke 1997), *D. menziesii* and *D. anceps* start to grow only under short day conditions in late winter/spring, even under the sea ice. They reach maximal growth rates in spring (September for *D. anceps* and December for *D. menziesii*) and have their minimum growth activity in summer to autumn (from January to May; Wiencke 1990; Gómez and Wiencke 1997). Our experiments—due to logistical constraints—took place in the Antarctic summer and unfortunately growth was very low due to the circannual growth rhythm of the two species, possibly masking treatment effects. However, not just season but also other factors such as age and size of the algae may influence growth rates, as it has been found in other studies (e.g. Khailov 1976; Wiencke 1990; Zacher et al. 2016). Current and modelled warming in Antarctica (Clark et al. 2013) does not seem to threaten the ecosystem builders *D. anceps* and *D. menziesii* as growth until 7 °C is not reduced compared to lower temperatures and material was healthy without any bleaching. Upper survival temperature (UST) of *D. anceps* is published to be around 11–12 °C (Wiencke and tom Dieck 1989). Preliminary results suggest that the UST of *D. menziesii* may be higher compared to *D. anceps* (Matula unpublished), which would also explain its broader distribution compared to *D. anceps* (Wiencke et al. 2014.).

Irradiance effects on photosynthesis

Not surprisingly, irradiance exerted the strongest effects on photosynthetic parameters of *D. menziesii* and *D. anceps*. F_v/F_m in both species is significantly higher at 10 µmol m^{-2} s^{-1} than at 100 µmol m^{-2} s^{-1}, pointing to a light stress at the higher irradiance conditions. In contrast, $rERT_{max}$ and E_k are higher at 100 than at 10 µmol m^{-2} s^{-1}, though only statistically significant in *D. menziesii*, pointing to acclimation to higher irradiance. The irradiance regime in Antarctica is highly variable—from complete darkness in winter under sea ice to maximum PAR values between 230 and 500 µmol m^{-2} s^{-1} (at 10 and 5 m, respectively) in spring, under clear water conditions (Campana et al. 2018; Deregibus pers. comm.). Algal photosynthesis in Antarctica is therefore restricted from spring to autumn (Wiencke et al. 2009). Major seasonal adjustments of photosynthesis include changes in photosynthetic efficiency (initial slope, α) and particularly the light requirements for saturation (E_k) (Gómez et al. 2009, 2019; Wiencke et al. 2009). Both *Desmarestia* species showed a high acclimation potential to these changing environmental light conditions in our study. E_k values measured were well above 100 µmol m^{-2} s^{-1} for both species and all treatments, which is higher than most published values. Weykam et al. (1996) measured E_k values of 32 and 30 µmol m^{-2} s^{-1} for *D. anceps* and *D. menziesii*, respectively, whereas Gómez et al. (2009) reviewed values between 31 and 105 µmol m^{-2} s^{-1}. In another study,

Table 2 Experiments 1 and 2: Repeated Measurements ANOVA of F_v/F_m, α (in µmol m^{-2} s^{-1}), $rETR_{max}$ and E_k (in µmol m^{-2} s^{-1}) of *Desmarestia menziesii* (DM) and *D. anceps* (DA) on irradiance (10 and 100 µmol m^{-2} s^{-1}, experiment 1), temperature (2 and 7 °C, experiment 2) and culture treatment (mono and co-cultures) effects over time ($n=5$)

E	Species	Source of variation	F_v/F_m			$rETR_{max}$			α			E_k		
			df	*F* value	*p* value	*df*	*F* value	*p* value	*df*	*F* value	*p* value	*df*	*F* value	*p* value
1	DM	LI	1	37.411	*<0.0001*	1	16.272	*0.001*	1	1.142	ns	1	22.706	*0.0002*
		CU	1	0.131	ns	1	1.885	ns	1	0.192	ns	1	1.693	ns
		LI x CU	1	0.621	ns	1	2.637	ns	1	1.548	ns	1	1.428	ns
		TI	2	17.596	*<0.0001**	2	4.375	*0.02*	2	5.562	*0.01*	2	2.430	ns
		TI x LI	2	6.780	*0.0003**	2	0.102	ns	2	2.285	ns	2	0.312	ns
		TI x CU	2	0.280	ns	2	7.289	*0.002*	2	2.742	ns	2	4.025	*0.03*
		TI x LI x CU	2	1.990	ns	2	0.971	ns	2	0.405	ns	2	0.491	ns
	DA	LI	1	85.911	*<0.0001*	1	1.483	ns	1	1.765	ns	1	3.177	ns
		CU	1	0.000	ns	1	0.073	ns	1	0.048	ns	1	0.006	ns
		LI x CU	1	0.000	ns	1	0.923	ns	1	3.155	ns	1	0.368	ns
		TI	2	19.604	*<0.0001**	2	8.642	*0.001*	2	12.685	*<0.0001*	2	4.553	*0.02*
		TI x LI	2	11.227	*<0.0001**	2	1.131	ns	2	3.3901	*0.03*	2	0.098	ns
		TI x CU	2	1.623	ns	2	0.323	ns	2	0.077	ns	2	0.467	ns
		TI x LI x CU	2	1.301	ns	2	0.062	ns	2	0.078	ns	2	0.710	ns
2	DM	TE	1	3.740	ns	1	2.643	ns	1	0.060	ns	1	7.191	*0.02*
		CU	1	0.350	ns	1	1.316	ns	1	0.541	ns	1	1.805	ns
		TE x CU	1	0.010	ns	1	0.029	ns	1	0.779	ns	1	0.698	ns
		TI	2	21.310	*<0.0001*	2	7.450	*0.002*	2	3.104	ns	2	7.731	*0.002*
		TI x TE	2	11.630	*<0.0001*	2	0.709	ns	2	1.587	ns	2	0.525	ns
		TI x CU	2	0.570	ns	2	0.645	ns	2	0.865	ns	2	0.378	ns
		TI x TE x CU	2	2.470	ns	2	0.063	ns	2	1.023	ns	2	0.061	ns
	DA	TE	1	8.984	*0.009*	1	2.788	ns	1	3.116	ns	1	1.505	ns
		CU	1	2.292	ns	1	0.921	ns	1	0.967	ns	1	0.719	ns
		TE x CU	1	1.608	ns	1	2.550	ns	1	2.380	ns	1	1.581	ns
		TI	2	30.77	*<0.0001**	2	2.913	ns	2	0.603	ns	2	3.650	*0.04**
		TI x TE	2	6.421	*0.003**	2	0.037	ns	2	0.272	ns	2	0.548	ns
		TI x CU	2	0.510	ns	2	0.125	ns	2	0.042	ns	2	0.229	ns
		TI x TE x CU	2	0.535	ns	2	0.140	ns	2	0.462	ns	2	0.092	ns

LI = irradiance intensity, CU = culture treatment, TE = temperature, TI = time, ns = not significant. Significant values in italics. Greenhouse–Geisser corrections for departure from sphericity with asterisk

p values were set to < 0.5

Table 3 Experiments 1 and 2: Repeated Measurements ANOVA of F_v/F_m, α (in µmol m^{-2} s^{-1}), $rETR_{max}$ and E_k (in µmol m^{-2} s^{-1}) of *Desmarestia menziesii* (DM) and *D. anceps* (DA) mono-cultured during experiments 1 and 2 on species, irradiance and temperature effects over time ($n = 5$)

Species	E	Source of variation	F_v/F_m			$rETR_{max}$			α			E_k		
			df	*F* value	*p* value	*df*	*F* value	*p* value	*df*	*F* value	*p* value	*df*	*F* value	*p* value
DM + DA mono-cultured	1	SP	1	3.048	ns	1	29.28	*< 0.0001*	1	15.73	*0.001*	1	22.12	*0.0007*
		LI	1	63.29	*< 0.0001*	1	7.35	*0.015*	1	0.018	ns	1	9.18	*0.004*
		TI	1	31.79	*0.0001*	1	3.84	ns*	1	10.67	*0.009**	1	0.569	ns
		SP × LI	1	0.696	ns	1	0.001	ns	1	0.100	ns	1	0.070	ns
		TI × LI	2	29.22	*< 0.0001*	2	1.90	ns	2	5.67	ns*	2	0.231	ns
		TI × SP	2	1.50	ns	2	1.75	ns	2	0.855	ns	2	1.97	ns
		TI × LI × SP	2	1.27	ns	2	0.177	ns	2	0.012	ns	2	0.523	ns
	2	SP	1	2.05	ns	1	54.06	*< 0.0001*	1	58.24	*0.0002*	1	29.48	*0.0002*
		TE	1	14.42	*< 0.0001*	1	0.088	ns	1	3.545	*0.03*	1	0.088	ns
		TI	1	54.14	*< 0.0001*	1	3.344	*0.02*	1	0.481	ns	1	3.42	*0.03*
		SP × TE	1	0.440	ns	1	1.26	*0.02*	1	4.782	ns	1	9.89	*0.01*
		TI × TE	2	5.06	ns	2	0.115	ns	2	0.005	ns	2	0.249	ns
		TI × SP	2	2.11	ns	2	11.25	ns	2	4.782	ns	2	0.051	ns
		TI × TE × SP	2	0.47	ns	2	0.29	ns	2	0.829	ns	2	0.467	ns

p values were set to < 0.5

SP = Species (*D. menziesii* and *D. anceps*), LI = Light (10 and 100 µmol m^{-2} s^{-1}, experiment 2), TE = Temperature (2 and 7 °C, experiment 3), TI = time, ns = not significant. Significant values in italics. Greenhouse–Geisser corrections for departure from sphericity with asterisk

values between 56 and 121 µmol m^{-2} s^{-1} were measured for the two *Desmarestia* species, approaching the values we observed (Gómez et al. 2019). Furthermore, Schoenrock et al. (2015) measured E_k values similar and even higher than in our study, between 130 and 220 µmol m^{-2} s^{-1}. Interestingly, the in situ measurements taken in the field were only slightly higher than our findings (167 for *D. menziesii* and 141 for *D. anceps*). Variations with other studies can be due to three main reasons: (1) difference in the methodology: Weykam et al. (1996), Gómez et al. (1995) and Gómez and Wiencke (1997), for example, measured and calculated the E_k values using oxygen measurements via an optode, while the other studies used a fluorometer. (2) Season: as stated above, photosynthesis is highly seasonal in Antarctic macroalgae. Whereas Weykam et al. (1996) and Gómez and Wiencke (1997) measured field material sampled in austral spring, summer material was used in our study and in the study of Gómez et al. (2019) and Schoenrock et al. (2015). This material had a long time under high irradiance conditions to adjust its photosynthesis. (3) Sampling depth: It was shown by Gómez and Wiencke (1997) and Rautenberger et al. (2015) that especially *D. anceps* shows decreasing E_k values with depth. In this study, *D. anceps* was sampled at its upper distribution limit of 5 m. At this depth, Rautenberger et al. (2015) measured an E_k of 80 µmol m^{-2} s^{-1}, whereas at 15 m it was 50% less. Comparing our data to culture material, which was held in stock cultures under low irradiance conditions for many years, the differences are even more pronounced. E_k values varied between 7 and 26 µmol m^{-2} s^{-1} for *D. anceps* and 17 to 40 µmol m^{-2} s^{-1} in *D. menziesii* in culture material (Zacher et al. 2016). In our experiment, we worked with algae freshly taken from the field and tried to apply a realistic PAR scenario, comparable to the field values. The daily PAR doses algae may experience at the sample site at 5 m are, for example, 1130 (±500) kJ (measured in January 2014, Deregibus pers. comm.) which is very similar to our high irradiance treatment with 1300 kJ PAR. The α values, as a measure of electron transport efficiency, were between 0.26 and 0.42 µmol m^{-2} s^{-1} and were not significantly affected by irradiance during the experiment. Values measured in Weykam et al. (1996) were much higher (1.26 for *D. anceps* and 1.74 µmol m^{-2} s^{-1} for *D. menziesii*) from spring samples. In contrast, Schoenrock et al. (2015) found lower values in samples from late summer, with in situ values of 0.1 µmol m^{-2} s^{-1} for *D. anceps* and 0.134 µmol m^{-2} s^{-1} for *D. menziesii,* and Gómez et al. (2019) found even lower values, varying between 0.13 and 0.24 µmol m^{-2} s^{-1}. The photosynthetic efficiency (α) can greatly vary according to the season. For example, Gómez and Wiencke (1997) showed that the α parameter of *D. menziesii* presents highest values in winter–spring optimising photosynthesis under lower light conditions and minima in summer. As a higher α points to a more shade-adapted plant, this fits very well with the results of the E_k values (the lower the E_k, the more shade adapted) as well as being in line with the reduced $rETR_{max}$ under low irradiance conditions (less

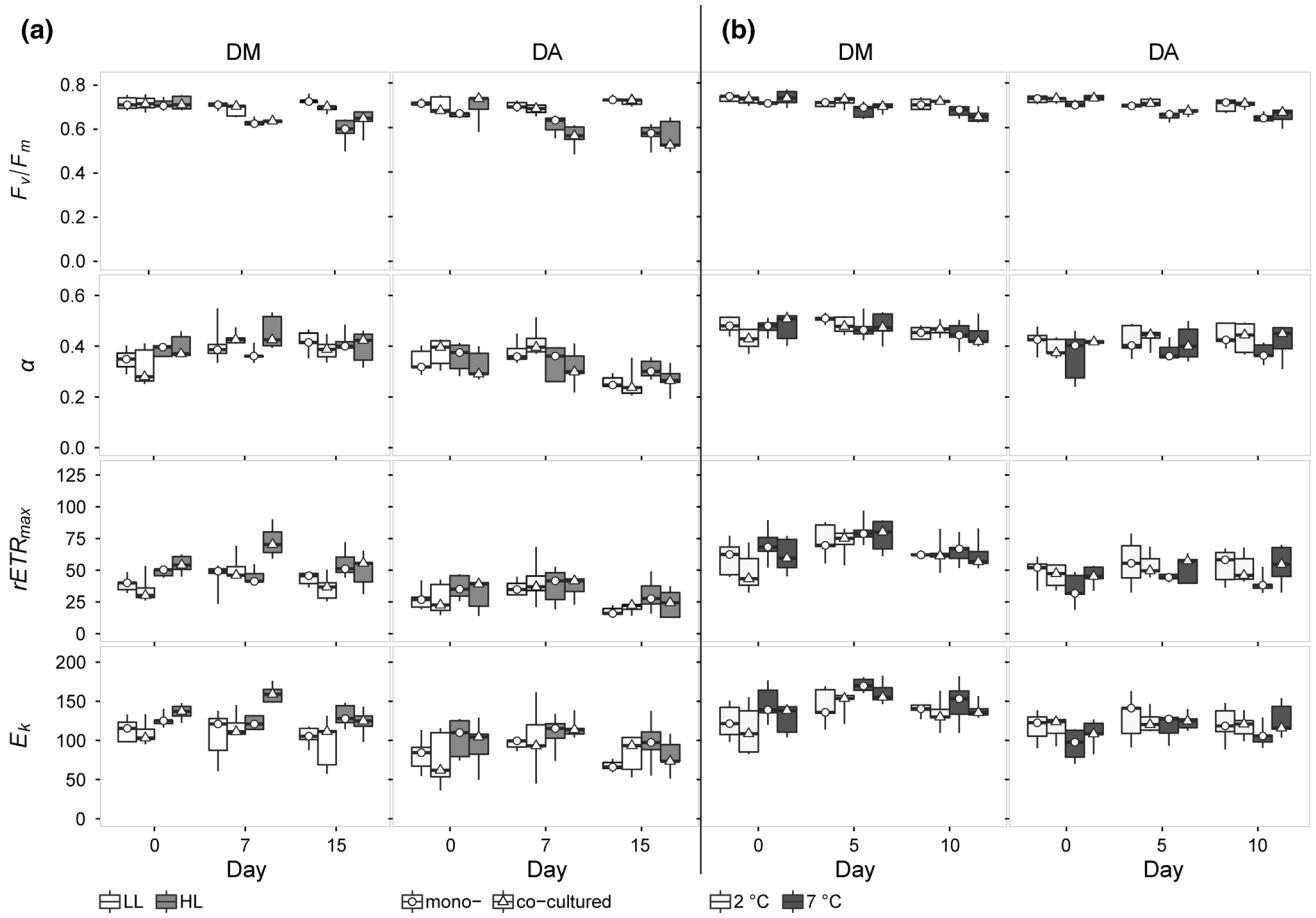

Fig. 3 Experiments 1 (**a**) and 2 (**b**): Box–whisker plots of maximum quantum yield (F_v/F_m), α (in µmol m^{-2} s^{-1}), $rETR_{max}$ and E_k (in µmol m^{-2} s^{-1}) of *Desmarestia menziesii* (DM) and *D. anceps* (DA) mono-cultured and co-cultured under 10 (LL) and 100 µmol m^{-2} s^{-1} (HL, experiment 1) or at 2 and 7 °C (experiment 2) (median ± 95 to 5 percentile, $n = 5$)

effective electron transport). Although both species are characterised as strongly shade adapted (revised in Gómez et al. 2009), they can also cope well with enhanced irradiance conditions occurring during Austral spring and summer. As for growth, a strong seasonal pattern of photosynthetic performance of macroalgae has been found as well in long-term studies (Weykam and Wiencke 1996; Gómez and Wiencke 1997; Weykam et al. 1997; Lüder et al. 2001, 2002) and in field experiments (Gutkowski and Maleszewski 1989; Drew and Hastings 1992; Gómez et al. 1995, 1997).

Temperature effects on photosynthesis

F_v/F_m was higher at 2 °C compared to 7 °C in *D. anceps* and *D. menziesii* (although not always significantly). E_k values, on the other hand, were higher at 7 °C than at 2 °C in *D. menziesii*. Furthermore, F_v/F_m decreased over time in the 7 °C treatment, while it did not in the 2 °C treatment. The higher F_v/F_m values at lower temperatures are in contrast to experiments with cultured material of *D. menziesii* and *D. anceps* where F_v/F_m was higher at 5 compared to 0 °C (Zacher et al. 2016). However, the E_k values showed the same trend, with higher values at higher temperatures (Zacher et al. 2016). While variation in the temperatures used in previous experiments renders a direct comparison difficult, a just 2 °C difference reversed the effect of the study of Zacher et al. (2016) and demonstrates again the strong cold-water adaptation of these alga (Gómez et al. 2009). Antarctic seaweeds have been shown to exhibit P_{max} values at 0 °C as high as temperate seaweeds measured at higher temperatures (Wiencke et al. 1993) due to a variety of adaptations to cold temperatures such as (i) unsaturated fatty acids that maintain the fluidity of the membranes, (ii) molecular adaptations of the enzymes to the cold, (iii) cold shock and antifreeze proteins and (iv) adaptations of the electron transport chain (reviewed in Morgan-Kiss et al. 2006). Although Antarctic macroalgae are strong cold-water-adapted species, it has also been shown that their optima for photosynthesis lie above the temperature of their natural environment at least in cultured algae (Wiencke et al.

1993; Gómez et al. 2009). This effect was not detectable in our experiment, as F_v/F_m is higher under colder temperature and $rETR_{max}$ was not affected by temperature. These observed differences may be due in part to the fact that field material and not culture material from long-time stock cultures was used, as well as interactive effects with other factors. Rautenberger et al. (2015), for example, did not find any difference in F_v/F_m in *D. anceps* and *D. menziesii* derived from field material comparing 2 and 7 °C treatment under short time exposure (22 h). Also Schoenrock et al. (2015) did not find strong differences in photosynthetic parameters of *D. anceps* and *D. menziesii* from field material exposed to 1.5 and 3.5 °C, supporting the idea that field material may react differently than culture material. Gómez et al. (2019) detected a small, but not significant reduction in F_v/F_m while exposing both *Desmarestia* species to UV radiation (UVR; 280–400 nm) and 7 °C compared to a control treatment without UVR and 2 °C. Using culture material, Zacher et al. (2016) detected an initial synergistic effect of high temperature (5 °C) and high irradiance (50 µmol m^{-2} s^{-1}) leading to lower F_v/F_m which disappeared during the second week of the experiment. Moreover, $rETR_{max}$ of *D. menziesii* decreased stronger at lower temperatures (0 °C) than at 5 °C, whereas *D. anceps* sporophytes responded in the opposite way. Also for the Arctic kelp *Saccharina latissima* (Heinrich 2016), the highest stress response was found for the combination of high temperature with high irradiance. Our experiments with field material were only run over 11 to 16 days, thus raising the possibility that high irradiance (100 µmol m^{-2} s^{-1}) in combination with higher temperatures led to a higher stress response of the algae compared to 2 °C and low light.

It is also postulated that brown algae with intermittent growth phases characterised by periods of growth followed by periods of rest over one year (Lüning and tom Dieck 1989), such as Laminariales, Fucales or Antarctic Desmarestiales (Wiencke 1990; Gómez and Wiencke 1997), may exhibit seasonally different temperature affinities (Zacher et al. 2016). For example, temperate brown algae of the order Laminariales and Desmarestiales were more susceptible to high temperatures during late winter compared to summer or in actively growing tissue compared to old tissue (Lüning 1984). In a recent seasonal benthocosm study on the temperate brown alga *Fucus vesiculosus*, Graiff et al. (2015) showed how major temperature effects were stronger during the active growth phase. This is of special interest in Antarctica where winter temperatures have been rising more than summer temperatures (Schloss et al. 2012). The large brown species of the order Desmarestiales thus have to endure a long dark winter period initiating growth during late winter by using the storage compounds built-up during spring–autumn.

Differences in the photosynthetic performance between *Desmarestia menziesii* and *D. anceps*

Comparing F_v/F_m of *D. anceps* and *D. menziesii* monocultured, no difference was detected. It was generally above 0.7 under non-stressful conditions, very similar to values measured in other studies (Rautenberger et al. 2015; Schoenrock et al. 2015). However, $rETR_{max}$, E_k and α were always higher in *D. menziesii* than in *D. anceps,* irrespective of the temperature or irradiance applied. In particular, the higher $rETR_{max}$ and E_k values in *D. menziesii* (in some cases double) compared to *D. anceps* may explain, at least partly, the dominance of the first species over the latter in shallower habitats. While *D. menziesii* is dominant around 5 m, *D. anceps* dominates at 10 m (Quartino et al. 2001). *Desmarestia menziesii* needs more light to saturate its photosynthesis but may use all this energy to build up biomass, whereas *D. anceps* seems to be more shade adapted. Unfortunately, we could not confirm this with the growth measurements (see above) and no comparable growth data for both species under high irradiance exist as most studies applied low irradiances < 20 µmol m^{-2} s^{-1} (Rautenberger et al. 2015; Schoenrock et al. 2015). Young sporophytes of *D. anceps* were shown to grow well under 50 µmol m^{-2} s^{-1} (Wiencke and tom Dieck 1989) but no comparative studies with *D. menziesii* exist to our knowledge. However, both species are able to adjust their photosynthetic performance very fast to different irradiance conditions as stated above.

Effects of co-culturing

No co-culturing effects on growth nor on photosynthetic parameters between *D. menziesii* and *D. anceps* occurred in combination with different temperatures and irradiance regimes. The same result was found in a similar study performed with cultured material, where *D. menziesii* and *D. anceps* were mono- and co-cultured under different temperatures (Zacher et al. 2016). Although the outcome of these experiments did not show any co-culturing effect between these species, competition may occur on a different time scale (longer experimental time) or in different life-cycle stages and/or under different environmental conditions (Carpenter 1990; Coelho et al. 2000; Barner et al. 2016; Traiger and Konar 2017). Nabivailo et al. (2014) and Xu et al. (2013) conducted experiments with different life-cycle stages (gametophytes, adult thalli) and showed both negative and positive interactions. In Arctic kelps, competition occurs during early recruitment (gametophyte and young sporophyte stage) and can be altered by the temperature regime depending on the temperature optima of the competing species. Generally, early developmental stages, such as young sporophytes, seem to be affected by

biotic or abiotic alterations in a species-specific manner (Zacher et al. 2016); therefore in future studies, different life-stages of our tested algae and longer experimental durations need to be taken into account.

Conclusion

Although a temperature increase of 7 °C in summer is not lethal for *D. menziesii* and *D. anceps* sporophytes, the higher temperature exerted a stress response on their photosynthetic efficiency in combination with irradiance intensities encountered under field conditions (50 to 100 µmol m^{-2} s^{-1}). Sporophytes of *D. menziesii* show better physiological abilities to cope with high temperature and irradiance regimes compared to *D. anceps* ones, as a confirmation of our initial hypothesis. However, no co-cultivation effect was found in this study within the two species, possibly due to the low growth rates of both species. Future experiments need to take into consideration the combined effects of other relevant factors (such as temperature, irradiance, nutrients, competition and grazing), which may act in a synergistic or antagonistic way over different time spans (short- and long-term exposure). Further investigations on all life-cycle stages (spores, gametophytes, young and adult sporophytes), reproduction (e.g. gametogenesis) and in different seasons would be important to generate a more complete picture and to better understand the effects of these threats on species and macroalgal assemblages in general. The seasonal aspect is of particular concern because these algae mainly grow in late winter/spring when temperature rise through global warming is highest (Schloss et al. 2012). Contrasting results between laboratory and field material experiments (Wiencke and tom Dieck 1989; Rautenberger et al. 2015; Zacher et al. 2016) highlight the need for more field-based research and show that care must be taken in extrapolating small-scale laboratory experiments to the community level.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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