UNIVERSITE PIERRE ET MARIE CURIE

Thèse de Master
Année 2015-2016

Mention Sciences de l'Univers, Environnement, Ecologie
Spécialité Océanographie et Environnements Marins

Effects of interspecific competition and global warming on endemic Antarctic *Desmarestia* species

Valentina Savaglia

Réalisé sous la responsabilité de Katharina Zacher
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30 pages

Nombre des figures : 10

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Symbols/ Abbreviations	**Description**	**Units (S.I.)**
Chl *a*	Chlorophyll a concentration	µg/100 µL
E_k	Irradiance at which photosynthesis is saturated	µmol photons.m^{-2}.s^{-1}
E_{PAR}	Irradiance in the PAR region	µmol photons.m^{-2}.s^{-1}
F'_m	Maximal fluorescence yield in light-adapted state	
F_0	Minimum fluorescence yield in dark-adapted state	
F_m	Maximal fluorescence yield in dark-adapted samples	
F_v/F_m	Quantum yield of PSII photochemestry in the dark-adapted state	
HI	High irradiance	µmol photons.m^{-2}.s^{-1}
LI	Low irradiance	µmol photons.m^{-2}.s^{-1}
PAR	Photosynthetically Active Radiation (400 – 700 nm)	µmol photons.m^{-2}.s^{-1}
P-E	Photosynthesis-irradiance curve	
PSII	Photosystem II	
PSU	Practical salinity unit	

Symbol list

rETR	Relative electron transport rate	µmol photons.m^{-2}.s^{-1}
$rETR_{max}$	Maximum relative electron transport rate	µmol photons.m^{-2}.s^{-1}
UST	Upper Survival Temperature	°C
WW	Wet weight	g
α	Slope of the light-limited region of the P-E curve	µmol photons.m^{-2}.s^{-1}

I. Introduction

The Western Antarctic Peninsula (WAP) has been described as an area highly vulnerable to the effects of climate change (Clarke et al. 2007, IPCC 2013, Ducklow et al. 2013, Turley 2013). This region is experiencing one of the fastest warming rates in the world (Turner et al. 2009b), with an increasing average of air temperature of 0.5 °C per decade (Turner et al. 2009a). At Potter Cove (King George Island, WAP) average water temperatures increased by 0.32 °C per decade and winter sea surface temperatures even increased by more than 2 °C between 1991 and 2006 (Schloss et al. 2012). Therefore, the glacial systems is showing a direct response to the higher temperatures with a marked melting which contributes to reduce the light availability due to increasing sediment input (Schloss et al. 2012) causing strong impacts on local ecosystem communities.

The sublittoral rocky shores at the WAP are colonized by dense populations of seaweeds, which build highly complex and productive underwater forests (Wiencke et al. 2014). The order Desmarestiales (Phaeophyceae) is the dominant taxonomic group (Amsler et al. 1995, Quartino & Boraso de Zaixso 2008). These seaweed communities play a key role in the Antarctic coastal system, similar to Laminariales (kelp) communities along temperate to Polar rocky coasts of the Atlantic and Pacific Ocean (Clayton 1994). The cold-temperate Antarctic *Desmarestia menziesii* J. Agardh 1848 and the Antarctic endemic *Desmarestia anceps* Montagne 1842 form the highest macroalgal biomass in Antarctic coastal areas (together with *Himantothallus grandifolius*; Amsler et al. 1995, Brouwer 1996) with maxima of 10 kg fresh weight m^{-2} at some sites (Quartino & Boraso de Zaixso 2008, Gómez et al. 2009). The cold-temperate Antarctic *Iridaea cordata* (Turner) Bory de Saint-Vincent 1826 as the rest of red algae are unlikely to be dominant in terms of biomass, with the exception of the Antarctic endemic *Palmaria decipiens* (Reinsch) R. W. Ricker 1987 which can be a dominant or co-dominant species in shallow waters (Amsler personal observations, DeLaca & Lipps 1976, Chung et al. 1994, Klöser et al. 1996). It is speculated that seaweeds may be a much more important – year round – carbon source for the Antarctic benthos than in temperate seas (Reichardt 1987, Schloss et al. 2002). Furthermore, as ecosystem engineers they provide habitat and structural refuges for a vast amount of organisms such as amphipods, epi- and endophytes (Huang et al. 2007). The general zonation pattern of these large brown algae is relatively consistent over various sites in Antarctica with *D. menziesii*

dominating the shallow sublittoral between 3 and 5 meter followed by *D. anceps*, dominant at deeper sites around 10 m with both species co-occurring at all depths (Quartino 2001, Wiencke et al. 2014). At some sites, however, only one of these species is present (Wiencke et al. 2014). On King George Island the upper sublittoral is dominated by *D. menziesii* and *P. decipiens* is commonly competing with *I. cordata* (Becker et al. 2011). It is not clear what the structuring forces for this zonation are although the wide specific depth zonation ranges of the dominant brown macroalgae can be explained by the available irradiance constraint, with the range extending deeper in relatively exposed areas with clearer open ocean water compared to relatively protected areas with greater turbidity due to glacial melt and/or with more frequent ice cover (Amsler personal observations, DeLaca & Lipps 1976, Brouwer et al. 1995). Wave exposure, substrate type and bottom topography also influence macroalgal zonation and species occurrence (Klöser et al. 1996) but surely others, still unknown factors shape the local algal distribution (Wiencke et al. 2014).

Besides the regulatory role of abiotic factors, interspecific competition is often considered to be the major selective force in algal communities determining diversity, species distribution and the biomass of algal communities (Nabivailo & Titlyanov 2006). Competition has emerged as one of the dominant processes dictating assemblage structure (Barnes & DeGrave 2002) and especially in high latitudes is very little studied. Interspecific relationships among benthic seaweeds have scarcely been investigated in other world areas (see Reed 1990, Nabivailo et al. 2014, Xu et al. 2013) but just recently the question has been tackled also to polar seaweeds (Zacher et al. 2016). Even less information is available on the interplay of abiotic and biotic conditions which are fundamental for understanding the succession of macrophytobenthic communities (Nabivailo et al. 2014). 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 & Lubchenco 1990).

The Antarctic endemic members of the order Desmarestiales are characterized by very low light and temperature demand for growth, photosynthesis and reproduction, and their diverse regulative physiological characteristic allow them to complete their life cycle *in situ* at temperatures close to 0 °C and under very fluctuating irradiance intensities (Wiencke et al. 2007, Gómez et al. 2009 and references therein). However, the upper survival

temperature (UST) can be much higher for these species, normally according to their distribution (Wiencke & tom Dieck 1989; Wiencke 1994). Much of the available information on optimal irradiance conditions for polar seaweeds comes from photosynthesis-irradiance (*P-I*) curves. In general, polar seaweeds have high photosynthetic efficiency and hence low light requirement for photosynthesis, as determined by low E_k and high α values, which is an indicator of the photosynthetic efficiency at low irradiances (Henley 1993). Since growth, photosynthesis, reproduction and survival of all seaweeds are strongly affected by temperature and light (Lüning 1990, Wiencke et al. 1993, Gomez 1997), it is expected that further global warming will change the community composition and species distribution ranges of seaweed communities (e.g. Müller et al. 2009, Deregibus et al. 2016) with subsequent cascading effects through the food webs (Clarke et al. 2007, Ducklow et al. 2013). For the Arctic recent evidence supports these assumptions (Paar et al. 2015, Bartsch et al. 2016).

Polar regions are characterized by strong seasonal variations on light conditions. Around the Antarctic Peninsula, sea ice breaks up between early September and late November with increasing daylenghts and irradiance due to very high transparency of waters during spring. In early summer, however, light penetration through the water is reduced due to shading by phytoplankton blooms and suspended sediments (Drew & Hastings 1992; Klöser et al. 1993). Therefore, many polar seaweed species synchronize their growth phases and photosynthetic performances with the annual course of photoperiod (Wiencke 1990a, b, Gómez and Wiencke 1997). Both, *D. anceps* and *D. menziesii* are so called “season anticipators”, reproducing in winter, initiating growth under short day conditions in late winter-early spring and reducing growth during late summer (Wiencke 1990a, Gómez & Wiencke 1997). Because of the strong seasonal pattern, photosynthesis is mainly restricted to the spring-autumn period in these regions (Wiencke et al. 2009). Major seasonal adjustments of photosynthesis include species-specific changes of photosynthetical efficiency (α versus irradiance function) and particularly the light requirements for saturation (E_k) and compensation (E_c) of photosynthesis (Wiencke et al. 1993).

Former investigations indicated the lack of multifactorial studies when evaluating the fate of the unique Polar ecosystem (Wiencke et al. 2006). 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 competition may modify algal

responses, and are not yet understood at all. Therefore, the major aim of this investigation was to investigate for the first time the interaction of temperature combined with irradiance intensity and interspecific competition on growth and photosynthetic efficiency of the two endemic Antarctic macroalgae *D. menziesii* and *D. anceps*, either cultivated alone or co-cultivated.

II. Material and Methods

Sampling site. Three experiments were carried out at the German-Argentinean Dallmann Laboratory, Carlini Base, Potter Cove, King George Island, South Shetlands Islands, Antarctica (62°14'S-58°38'W; Deregibus et al. 2015, http://dx.doi.org/10.1594/PANGAEA.853859). An overview of the abiotic and biotic conditions of the Potter Cove ecosystem is given in e.g. Zacher (2007) and Schloss et al. (2002). Field material of the investigated algae was collected a few days before each experiment from Area A1 ("Peñón de Pesca", 62°23'S, 58°72'W; Deregibus et al. 2015) by scuba divers at 5 m during the Antarctic summer January-February 2016.

Algal material. Sporophytes of *Desmarestia menziesii*, *D. anceps* (experiments 1, 2 and 3), *Iridaea cordata* and *Palmaria decipiens* (only experiment 1), were collected with the holdfast and brought to the laboratory in dark boxes filled with seawater in order to avoid stress during transport. Prior to the start of the experiments, the individuals were kept in constantly aerated seawater containers under low irradiance conditions (~ 10 µmol photons m^{-2} s^{-1}) at 3 ± 1 °C. A day:night cycle of 16:8 hours was maintained prior and during each experiment, simulating long-day conditions. Individuals from each species were maintained separately. The seawater acquired from Potter Cove was changed daily. After a few days, algal individuals were cleaned from epiphytes and 10-20 cm of the apical parts of *Desmarestia* sporophytes were cut off with a sterile razor blade in order to have individuals of similar initial wet weight and size. Small individuals of similar sizes of *P. decipiens* and *I. cordata* were selected for the first experiment. Prior and after each experiment, pictures and lengths were taken to monitor the development of every specimen.

Experiment 1. Impact of interspecific competition and temperature on D. menziesii

Experimental set-up. Four days after the collection, algal material was transferred into 32 aerated 2L transparent plastic beakers filled with filtered (Durapore® Cartridge Filter, 0.22 µm) seawater of a salinity of ~ 32 PSU enriched with Provasoli medium (50 mL per 10 L of

seawater; Provasoli 1968). Seawater was exchanged every week in order to avoid nutrient depletion. In a two-factorial design (Table 1) the effect of (1) temperature (2 °C = ambient summer temperature vs. 7 °C= global warming scenario) and (2) culture treatment (*D. menziesii* mono- vs. co-cultured) over a period of 14 days (from day 0 to day 14) was tested. Algal material was previously acclimated to the experimental conditions for three days (from day -3 to day 0). *Desmarestia menziesii* was co-cultured with the three different species *D. anceps, P. decipiens* and *I. cordata*. Each experimental condition was replicated in four beakers (n = 4), containing 2 sporophytes each (of the same species for the mono-cultured and of two species for the co-cultured treatments). The beakers were placed in temperature-controlled water baths (Variostat® CC, Huber, Germany) on day -3, providing temperatures of 2 and 7 °C (two bathes per temperature; 8 beakers in each tank; 16 beakers per temperature). Temperature was monitored via data loggers (Hobo Pendant® Temperature/Light Data Logger, USA). Due to technical problems, short time peaks of increased temperatures occurred during the experiment (on day -1 an increase of 2 °C was measured in one of the 2 °C bathes and on days 9 and 11 an increase of 3 °C was registered in one of the 7 °C bathes). Photosynthetically active radiation (PAR, 400-700 nm) was applied by 4 halogen OSRAM L36W/965 lamps (Bioloux, München, Germany), one over each bath, and was measured using a LI-COR LI-250A Light Meter (LI-COR, Inc., Lincoln, USA). The irradiance was set on day -3 to 100 µmol photons m^{-2} s^{-1} according to field measurements in Antarctica, representing the light at 5 m depth, where the biomass maximum of *D. menziesii* occurs (Quartino et al. 2001).

Table 1. Experimental set-up and treatment conditions of experiment 1-3.

Exp	Species	Temp (°C)		Day lenght	Irradiance (µmol m^{-2} s^{-1})		Experimental period	Acclimation time	Measured Variables
1	*D. menziesii, D. anceps, I. cordata, P. decipiens*	2	7	16:8	100		14 (day 0 to day 14)	3 (day -3 to day 0)	• WW (mg) • F_v/F_m
2	*D. menziesii, D. anceps*	2		16:8	10	100*	16 (day 0 to day 16)	4 (day -4 to day 0)	• WW (mg) • F_v/F_m • *P-I* curves • Pigments
3	*D. menziesii, D. anceps*	2	7	16:8	50		11 (day 0 to day 11)	3 (day -3 to day 0)	• WW (mg) • F_v/F_m • *P-I* curves • Pigments

*High irradiance for the 2nd experiment was set from day 0, after 3 days of acclimation days to low irradiance.

Growth measurements. Pre-experimental wet weight (WW, mg) was measured the day the algal material was transferred into the beakers (day -3). Later on, wet weight was measured one day before starting the experiment (day -1; initial) and then on day 6 and 14 by carefully blotting each sporophytes one by one with tissue paper before weighing (Sartorius CPA323S-0CE, Germany). Overall growth rate were calculated as:

$$specific\ growth\ rate\ (\%\ d^{-1}) = 100\ \frac{lnN_t\ N_0^{-1}}{t}$$

Where N_0 = initial WW, N_t = WW on day t, and t = time period expressed in day (see also Wiencke and tom Dieck 1989). Overall growth rate was measured from day -1 (initial) to day 14.

Photosynthetic efficiency. Photosynthetic efficiency of each sporophyte was measured as a maximum quantum yield of photosystem II (PSII) using a PAM 2100 chlorophyll *a* fluorometer (Walz GmbH, Effeltrich, Germany) connected to a PC running PamWin™ software. Maximum quantum yield of PSII after 3 minutes of dark adaptation was calculated by the PAM software as:

$$F_v/F_m\ = (F_m - F_0)/\ F_m$$

Three minutes of dark incubation were chosen because no differences were encountered in experimental testing measurements of F_v/F_m after 3, 5, 7, 10 and 15 min dark adaption.

Prior to the beginning of the experiment (day -3), pre-experimental measurements of the maximum quantum yield (F_v/F_m) took place. Later on, F_v/F_m was measured on day 1 (Initials), 4, 7, 10 and 14. For the measurement, the fiber optic was placed at ~ 1 cm from the algae during each measurement. After a saturating light pulse (0.8 s; 600 ms completely saturating white light pulse) macroalgal specimens were dark adapted for 3 min, minimal (F_0) and maximal (F_m) fluorescence allowed calculating F_v/F_m, as described above.

Statistical analysis. Pre-experimental measurements of wet weight and maximum quantum yield were tested with a one-way ANOVA within each species to check for differences on algal material. Overall growth rate was tested with a two-way ANOVA in order to assess the effect of temperature and culture treatments on *D. menziesii*. Later on a one-way ANOVA was separately performed on overall growth rate of *D. menziesii*, *D. anceps*, *I. cordata* and *P. decipiens* to check differences due to the temperature effect. Repeated

measures (RM) ANOVA was performed for F_v/F_m of each species during the experimental duration (5 measurements in 14 days). Homogeneity of variances was tested using Levene's Test and heteroscedastic data were log transformed. If no homogeneity of variance could not be achieved it is marked in the tables. Where Mauchleys test of sphericity was violated (RM ANOVA), a Greenhouse-Geisser (G-G) correction was applied. Post-hoc multiple means comparisons were performed with a Tukey's Test. All tests were run using Statistica™ 6.0 (StatSoft) software package.

Experiment 2. Impact of interspecific competition and irradiance on D. menziesii and D. anceps

Experimental set-up. Five days after the collection, algal material was transferred into 30 aerated 2L transparent plastic beakers filled with filtered (Durapore® Cartridge Filter, 0.22 µm) seawater of a salinity of ~ 32 PSU enriched with Provasoli medium (50 mL per 10 L of seawater; Provasoli 1968) and germanium dioxide (0.5 mL of GeO_2 per liter of seawater as described by Shea and Chopin 2007), in order to avoid nutrient depletion and to inhibit diatom growth. Seawater was renewed every week. In a two-factorial design (Table 1) the effect of (1) irradiance intensity (low, LI = 10 µmol m^{-2} s^{-1} vs. high, HI = 100 µmol m^{-2} s^{-1}) and (2) culture treatment (*D. menziesii* and *D.* anceps mono- vs. co-cultured) over a period of 16 days (from day 0 to day 16) was tested. Each experimental condition was replicated in five beakers (n = 5), containing 2 sporophytes each (of the same species for the mono-cultured and of two species for the co-cultured treatments). The beakers were placed in temperature-controlled water tanks, providing a permanent temperature of 2 °C. Algal material was acclimated to 10 µmol photons m^{-2} s^{-1} and 2°C for four days (from day -4 to day 0) and raised to 100 µmol photons m^{-2} s^{-1} on day 0 in half of the beakers (two bathes per light; 7 or 8 beakers in each tank; 15 beakers per light). Temperature and photosynthetically active radiation were maintained and measured as previously described for the first experiment, but short term peaks of temperature were registered on day 6 due to technical problems (increasing up to 6.8 °C in one of the two LI treatments and up to 5 °C in one of the two HI treatments).

Growth measurements. Pre-experimental wet weight (WW, mg) was estimated on the first day of the acclimation period (day -4). Initial wet weight was measured on day -2 and then measurements took place on day 6, 13 and 16 as described for the first

experiment. Later on, overall growth rate was calculated as described for the first experiment.

Photosynthetic efficiency. Prior to the beginning of the experiment (day -4), measurements of the maximum quantum yield (F_v/F_m) on pre-experimental material under low irradiance took place as described for the first experiment. Later on, F_v/F_m was measured on day 0 (initials), 2, 7, 10 and 15. After the strong temperature increase (day 6), an extra measurement of F_v/F_m was performed and a stressed response was detected.
Additionally, three days prior to the experiment (day -3) and on day 15, rapid light curves were determined (PAM 2100). The effective PSII quantum yield for the illuminated samples was calculated 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. From these measurements, the relative electron transport rates of PSII (*rETR*) were calculated by multiplying the effective quantum yield of PSII (yield = $\Delta F/F'_m$) with the corresponding light intensity (E_{PAR} = irradiance in the PAR region; 400-700 nm) as following:

$$rETR = \Delta F/F'_m * E_{PAR}$$

To estimate photosynthesis irradiance (*P-E*) curve parameters, the hyperbolic tangent model (Jassby & Platt 1976) was applied to the low and high irradiance treatments for all the replicates, calculating α, as a measure for the electron transport efficiency, $rETR_{max}$ (rel. units), the maximum relative electron transport rate, and E_k (µmol photons m^{-2} s^{-1}), the saturation irradiance for electron transport (calculated as the intercept between α and the $rETR_{max}$ values). These parameters show the photosynthetic performance of the algae under the different treatments and may be used to interpret photo-acclimation.

Pigment composition. At the beginning and at the end of the experiment, pieces of ~ 200 mg (WW) from 10 individuals (5 for each species) were transferred in Eppendorf® tubes and fixed in liquid nitrogen. Ten extra samples were taken from the field and the same procedure was applied in order to calibrate the HPLC. Algae were stored at -20°C, freeze dried and stored at 5°C until leaving Antarctica. Pigment analysis took place in April 2016 at the University of Bremen, Germany. Each dried sample (~ 0,02 g) was weighted and transferred into 15 mL Falcon® round-bottom polypropylene tube (BD Biosciences, Sand Diego, CA, USA). Then, each tube was vortexed and centrifuged for 40 s (5m/s) in order to

pulverize into powder the algae before extraction. The pigments were extracted with 1000 µL of 90% acetone for 24 hours at 5 °C in the dark. The samples were then centrifuged for 5 minutes at 3000 rpm then. The supernatant was transferred to tubes by filtration with Nalgene® nylon syringe filters of 0.45 µm pore size (Nalge Nunc International, Rochester, NY, USA). The assessment of the pigment composition was performed by a reverse phase HPLC using LaChromeElite ® system equipped with a chilled autosampler L-2200 and a diode array detector L-2450 (VWR-Hitachi International GmbH, Darmstadt, Germany). For separating the pigments a Spherisorb® ODS-2 column (25 cm x 4.6 mm, 5 µm particle size; Waters, Milford, MA, USA) with a LiChropher® 100-RP-18 guard cartridge was employed snf s gradient according to Wright et al. (1991) applied. Peaks were detected at 440nm, identified, and quantified via co-chromatography with standards for chlorophyll *a*, chlorophyll c2, β-carotene and fucoxanthin (DHI Lab Products, Hørsholm, Denmark) together with the software EZChrom Elite ver. 3.1.3. (Agilent Technologies, Santa Clara, CA, USA).

Statistical analysis. Maximum quantum yield and wet weight were statistically analyzed as for the first experiment. Last day data of photosynthetic performance of *D. anceps* and *D. menziesii* ($rETR_{max}$, α and E_k) were tested in a two-way ANOVA for culture and irradiance effects for both species separately. Photosynthetic parameters of mono-cultured *D. menziesii* and *D. anceps* were also analyzed together in a one-way ANOVA for low and high irradiance effect in order to detect different behaviors between the two species under both irradiance conditions.

Experiment 3. Impact of interspecific competition and temperature on D. menziesii and D. anceps

Experimental set up. Two days after the collection, algal material was transferred into 30 aerated 2L transparent plastic beakers filled with filtered (Durapore® Cartridge Filter, 0.22 µm) seawater of a salinity of ~ 32 PSU enriched with Provasoli medium (100 mL per 10 L of seawater; Provasoli 1968) and germanium dioxide (0.5 mL of GeO_2 per liter of seawater as described by Shea and Chopin 2007), in order to avoid nutrient depletion and to inhibit diatom growth. Seawater was renewed every week. In a two-factorial design (Table 1) the effect of (1) temperature (2 °C = ambient summer temperature vs. 7 °C= global warming scenario) and (2) culture treatment (*D. menziesii* and *D. anceps* mono- vs. co-cultured) over a period of 11 days (from day 0 to day 11) was tested. Algal material was previously

acclimated to the experimental conditions for three days (from day -3 to day 0). Each experimental condition was replicated in five beakers (n = 5), containing 2 sporophytes each (of the same species for the mono-cultured and of two species for the co-cultured treatments). The beakers were placed in temperature-controlled water baths, under 50 µmol photons m^{-2} s^{-1} of irradiance (two baths per light; 7 or 8 beakers in each tank; 15 beakers per temperature). This irradiance intensity was selected because according to field measurements in Antarctica, it represents the mean summer light climate at 10 m depth, where both species occur (Deregibus, pers. comm.). Temperature and photosynthetically active radiation were maintained and measured as previously described for the first experiment. Short term peaks of temperature occurred on day 5 due to technical problems (an increase of 7°C was registered in one out of the two 2 °C treatments).

Growth measurements. Pre-experimental wet weight (WW, mg) was estimated on the first day of the acclimation period (day -3). Initial wet weight was measured on day -1 and then measurements took place on day 6 and 11 as described for the first experiment. Later on, growth rates and overall growth rate were estimated as described for the first experiment.

Photosynthetic efficiency. Prior to the beginning of the experiment (day -3), pre-experimental measurements of the maximum quantum yield (F_v/F_m) took place. Later on, F_v/F_m was measured on day 0 (initial), 2, 5 and 10. Additionally, the rapid light curves (*P-I* curves) were measured as described for the second experiment.

Pigment composition. Pigment content was analyzed with the same protocol used for the second experiment.

Statistical analysis. Maximum quantum yield and wet weight were statistically analyzed as for the first two experiments. Last day data of photosynthetic performance of *D. anceps* and *D. menziesii* ($rETR_{max}$, α and E_k) were tested in a two-way ANOVA for culture and temperature effects for both species separately. Photosynthetic parameters of mono-cultured *D. menziesii* and *D. anceps* were also analyzed together in a one-way ANOVA for low and high temperature in order to detect different behaviors between the two species.

III. Results

Experiment 1. Impact of interspecific competition and temperature on D. menziesii

Measurements of wet weight (WW) from pre-experimental material (day -4) were similar

at 2 and 7°C within *D. menziesii* and *I. cordata* (0.29±0.04 g; one-way ANOVA, F=0.808, p=0.36 fr *D. menziesii*; 0.36±0.1 g; one-way ANOVA, F=0.09, p=0.77 for *I. cordata*). In opposition, both *D. anceps* and *P. decipiens* individuals had a significant higher pre-experimental weight (one-way ANOVA, F=6.14, p=0.048 for *D. anceps*; F=7.68, p=0.03 for *P. decipiens*) at 2 compared to 7°C (0.35±0.02 g for *D. anceps* and 0.21±0.07 g for *P. decipiens* at 2°C; 0.3±0.04 g for *D. anceps* and 0.1±0.04 g for *P. decipiens* at 7°C). Overall growth rate of *D. menziesii* was not affected by temperature or culture condition (two-way ANOVA, F= 1.77, p= 0.19 for temperature; F= 1.9, p= 0.15 for irradiance; F= 1.28, p= 0.3 for interaction between temperature and culture; biomass showed in Annex 1; Fig. 1). While overall growth rate of *D. anecps* and *I. cordata* did not show any temperature effect (One-way ANOVA, F= 0.34, p= 0.91 for *D. anceps*; F= 3.6, p= 0.08 for *I. cordata*; biomass showed in Annex 1; Fig. 1), *P. decipiens* had a significantly higher overall growth rate at 7 compared to 2°C despite the fact that pre-experimental weight was higher at 2 than at 7°C (13.06±1.19 % d^{-1} at 7°C; 10.66±1.11 % d^{-1} at 2°C; one-way ANOVA, F= 8.73, p= 0.02; biomass showed in Annex 1; Fig. 1).

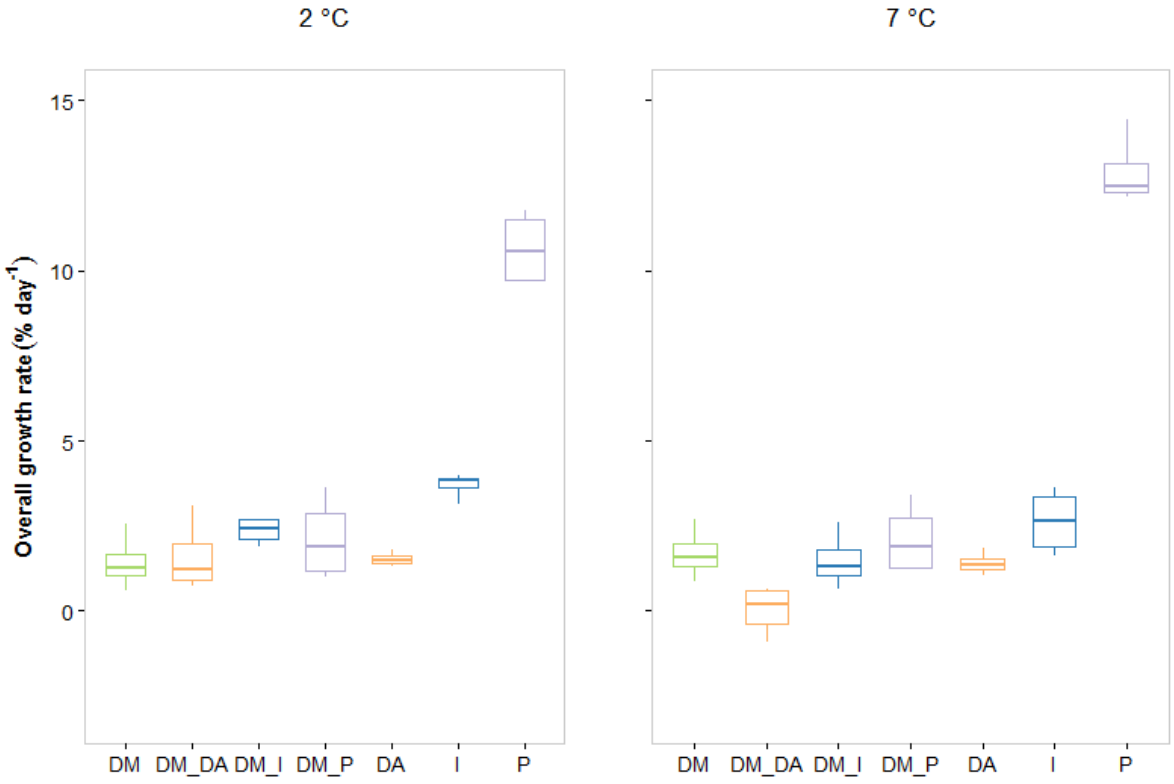


Fig.1 Box-whisker-boxplot of overall growth rate (% day^{-1}) of *Desmarestia menziesii* mono-cultured (DM) and co-cultured with *Desmarestia anceps* (DM_DA), *Iridaea cordata* (DM_I), *Palmaria decipiens* (DM_P) and *D. anceps* (DA), *I. cordata* (I) and *P. decipiens* (P) co-cultured with *D. menziesii* at 2°C and 7 °C (median ± 95 to 5 percentile, n=4).

Measurements of maximum quantum yield (F_v/F_m) from pre-experimental material (day -3) were not significantly different at both temperatures within each species. Pre-experimental F_v/F_m values for *D. menziesii* were 0.69±0.02, for *D. anceps* 0.61±0.09, for *I. cordata* 0.56±0.05, and for *P. decipiens* 0.49±0.03 (Fig.2). Generally, sporophytes of *D. menziesii* had a significantly higher maximum quantum yield at 2 compared to 7°C (RM ANOVA; Table2, Fig.2). During the experiment F_v/F_m of *D. menziesii, D. anceps* and *I. cordata* decreased significantly at both temperatures (day 0 to day 14; Table 2, Fig.2). Final values after 14 days of exposure were 0.61±0.06 for *D. menziesii*, 0.56±0.03 for *D. anceps* and 0.44±0.05 for *I. cordata* (Fig.2). *P. decipiens* showed the lowest F_v/F_m values compared to the other species during the experiment, but values stayed constantly low from day 0 to day 14 (0.40±0.06 in day 14; Table2, Fig.2).

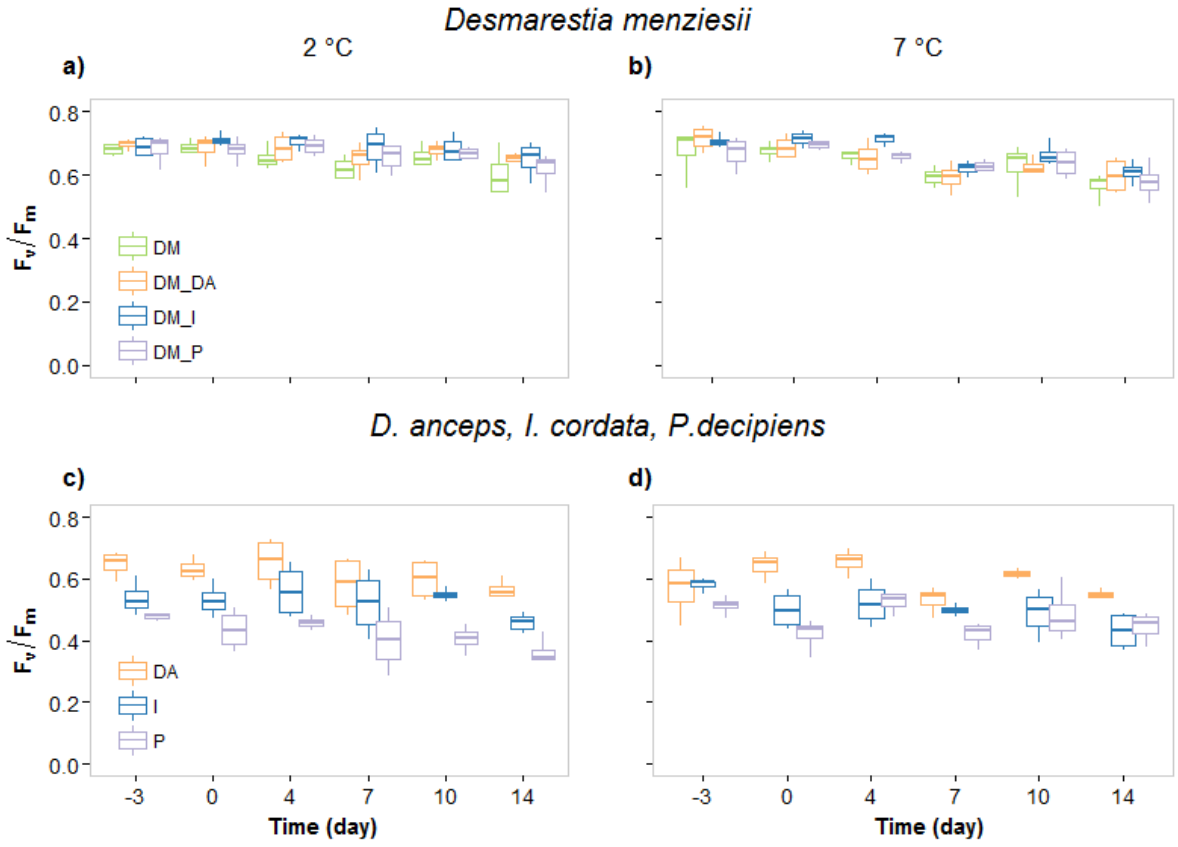


Fig.2 Box-whisker-plots of maximum quantum yield (*Fv/Fm*) of *Desmarestia menziesii* mono-cultured (DM) and co-cultured with *D. anceps* (DM_DA), *Iridaea cordata* (DM_I) and *Palmaria decipiens* (DM_P) at 2°C (a) and 7°C (b). Box-whisker-plots of maximum quantum yield (*Fv/Fm*) of *D. anceps* (DA), *I. cordata* (I) and *P. decipiens* (P) co-cultured with *D. menziesii* (c and d) (median ± 95 to 5 percentile, n=4).

Table 2. Repeated Measurements ANOVA of photosynthetic efficiency of *Desmarestia menziesii, D. anceps, Iridaea cordata* and *Palmaria decipiens* on temperature (2°/7°C) and culture treatments (mono/co-cultures, *D. menziesii* only) over time (*n*=4, 2 weeks). p-values were set to <0.05. TE = temperature, CU = culture treatment, TI = time, ns = not significant. Significant values in italics.

Species	Source of variation	F_v/F_m		
		df	F-value	p-value
Desmarestia menziesii	TE	1	5.98	*0.0222*
	CU	3	2.46	ns
	TE x CU	3	0.12	ns
	TI	4	27.89	*<0.0001*
	TI x TE	4	2.45	ns
	TI x CU	12	0.54	ns
	TI x TE x CU	12	0.39	ns
Desmarestia anceps	TE	1	0.0517	ns
	TI	4	9.8954	*<0.0001*
	TI x TE	4	0.9593	ns
Iridaea cordata	TE	1	1.2015	ns
	TI	4	3.2951	*0.0275*
	TI x TE	4	0.1465	ns
Palmaria decepiens	TE	1	4.924	ns
	TI	4	2.409	ns
	TI x TE	4	0.885	ns

Experiment 2. Impact of interspecific competition and irradiance on *D. menziesii* and *D. anceps*

Initial wet weight (WW) measurements from pre-experimental material (day -4) were similar for both *Desmarestia* species and both irradiance treatments (1.80±0.03 g; one-way ANOVA, F=2.72, p=0.11). Overall growth rate of *D. menziesii* and *D. anceps* was very low (0.23±0.31 % d-1 and 0.33±0.11 % d^{-1} for *D. menziesii* and *D. anceps* respectively; biomass showed in Annex 2) and not affected by irradiance (two-way ANOVA, F=3.60, p=0.07 for *D. menziesii*; F=0.69, p=0.42 for *D. anceps*) or culture treatment (two-way ANOVA, F=1.00, p=0.33 for *D. menziesii*; F=1.65, p=0.22 for *D. anceps*; Fig. 3).

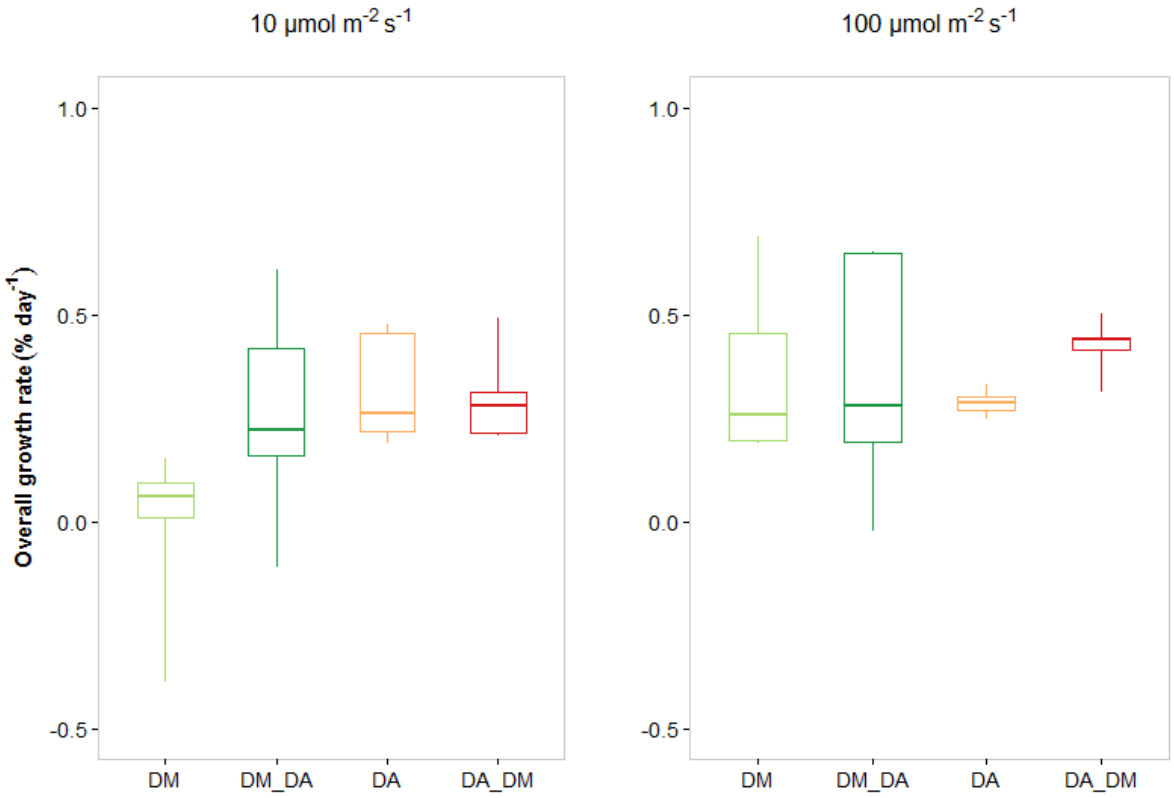


Fig.3 Box-whisker-plots of overall growth rate (% day^{-1}) of *Desmarestia menziesii* mono-cultured (DM) and co-cultured with *D. anceps* (DM_DA), *D. anceps* mono-cultured (DA) and *D. anceps* co-cultured with *D. menziesii* (DA_DM) under 10 and 100 µmol m^{-2} s^{-1} (median ± 95 to 5 percentile, n=5).

Measurements of maximum quantum yield (F_v/F_m) from pre-experimental material (still under low irradiance, day -3) were similar between both *Desmarestia* species and all treatments (0.74±0.03; one-way ANOVA, F=0.73, p=0.40; Fig. 4). In general, the maximum quantum yield of both species was significantly higher at low irradiance (10 µmol photons m^{-2} s^{-1}) compared to high irradiance (100 µmol photons m^{-2} s^{-1}) while no culture treatment effects were observed (Table 3). Although F_v/F_m values decreased over time in the high irradiance treatment to 0.61±0.07 in *D. menziesii* and 0.56±0.06 in *D. anceps* (day 15), they remained constant at low irradiances (0.71±0.03 and 0.72±0.02 for *D. menziesii* and *D. anceps* respectively on day 15), resulting in a significant time and irradiance interaction (Table 3, Fig. 4). Because both *Desmarestia* species initially showed similar F_v/F_m values, a comparison of both species after 15 days was possible (comparing mono-cultured treatments). At high irradiances the decrease of the F_v/F_m values in *D. menziesii* seem to be less pronounced than in *D. anceps*, however variances for some experimental days were still heterogeneous after transformation leading to consider this significant difference only as a trend (Table 3, Fig. 4).

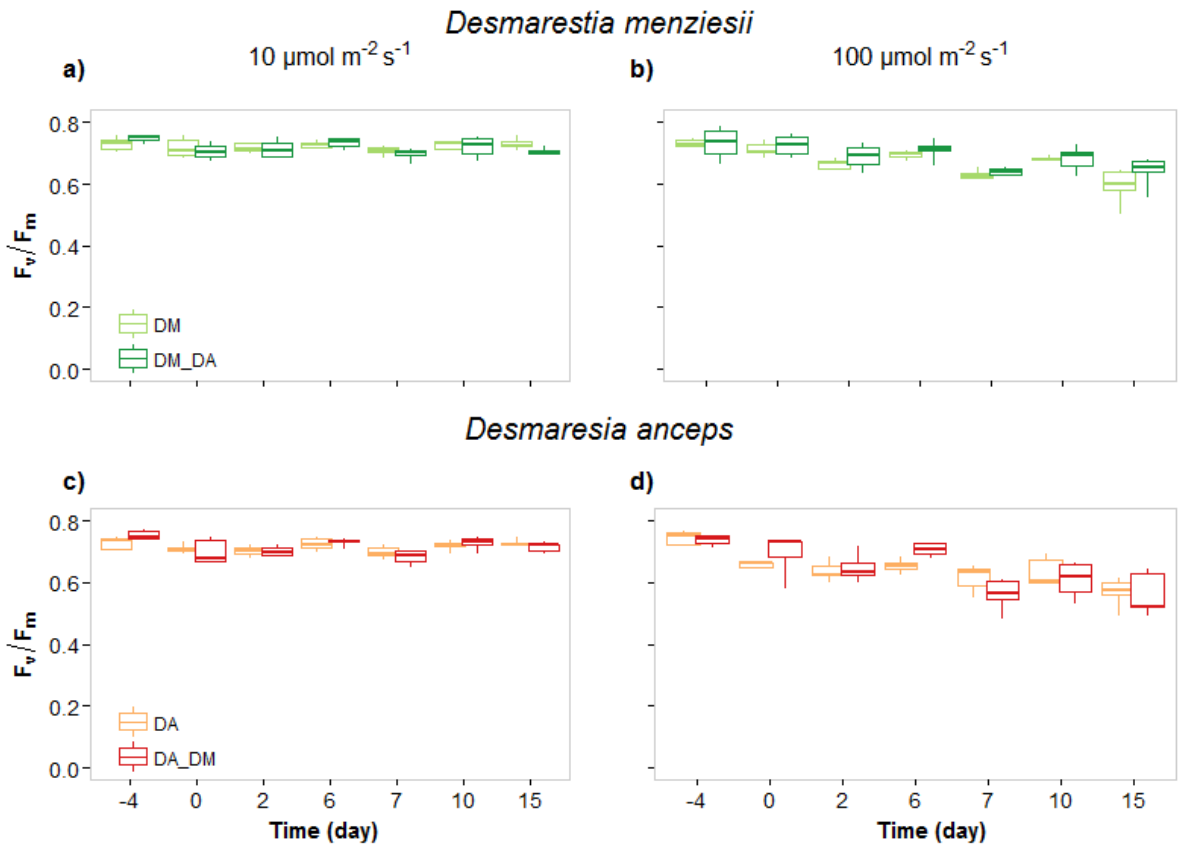


Fig.4 Box-whisker-plots of maximum quantum yield (*Fv/Fm*) of *Desmarestia menziesii* mono-cultured (DM) and co-cultured with *D. anceps* (DM_DA) (a and b), *D. anceps* mono-cultured (DA) and *D. anceps* co-cultured with *D. menziesii* (DA_DM) (c and d) under 10 and 100 µmol m^{-2} s^{-1} (median ± 95 to 5 percentile, n=5).

Comparing the photosynthetic efficiency between treatments on the last sampling day it was shown that $rETR_{max}$ of *D. menziesii* was significantly higher under high irradiance compared to the low irradiance treatment, while no culture effect was detected (two-way ANOVA, F= 6.11, p=0.02 for irradiance, Annex 4 for details; values in Annex 3; Fig. 5). α and E_k parameters *D. menziesii* were not affected by irradiance or culture treatments (two-way ANOVA, Annex 4 for details; values in Annex 3; Fig. 5). Similarly, $rETR_{max}$ and E_k parameters of *D. anceps* did not show any significant differences between the irradiance and the culture effects while α parameter showed higher values for the mono-cultures compared to the co-cultures under both irradiance intensities (two-way ANOVA, F= 9.28, p= 0.007; Annex 4 for details; values in Annex 3; Fig. 5). Comparing both species (mono-cultured) with each other it became evident that $rETR_{max}$ (only LL treatment) and E_k (both LL and HL treatments) were higher in *D. menziesii* compared to *D. anceps* (one-way ANOVA, Table 4; values in Annex 3; Fig. 5).

Table 3. a) Repeated Measurements ANOVA of maximum quantum yield (*Fv/Fm*) of *Desmarestia menziesii* and *D. anceps* mono- and co-cultured on irradiance (10/100µmol) and culture treatment (mono/co-cultures) effects over time (*n*=5, 2 weeks). b) Repeated Measurements ANOVA of maximum quantum yield (F_v/F_m) of *D. menziesii* and *D. anceps* mono-cultured on species effect (*D. menziesii*/*D. anceps*) over time (*n*=5, 2 weeks). LI = irradiance intensity, CU = culture treatment, SP = species, TI = time, ns = not significant, *a* = variances still heterogeneous after transformation. Significant values in italics.

	Species	Source of variation	F_v/F_m		
			df	F-value	p-value
a)	*Desmarestia menziesii*	LI	1	22.94	*0.0002*[a]
		CU	1	0.14	ns
		LI x CU	1	0.84	ns
		TI	4	12.57	*0.0001*
		TI x LI	4	9.04	*0.0005*
		TI x CU	4	0.30	ns
		TI x LI x CU	4	2.15	ns
	Desmarestia anceps	LI	1	51.12	*<0.0001*[a]
		CU	1	0.09	ns
		LI x CU	1	0.27	ns
		TI	4	9.68	*<0.0001*
		TI x LI	4	14.58	*<0.0001*
		TI x CU	4	1.49	ns
		TI x LI x CU	4	1.72	ns
b)	*Desmarestia menziesii* + *Desmarestia anceps*	LI	1	56.702	*<0.0001*[a]
		SP	1	4.860	*0.0425*[a]
		LI x SP	1	1.899	ns
		TI	4	8.204	*0.0008*
		TI x LI	4	13.328	*<0.0001*
		TI x SP	4	0.845	ns
		TI x LI x SP	4	1.209	ns

Sporophytes of *D. menziesii* and *D. anceps* used for pigment concentration analysis were not numerically enough to be statistically analyzed. However, Fig. 6 shows that after 15 days of exposure to high irradiance, pigment content (both chlorophyll *a* and fucoxanthin) increased in *D. menziesii* in contrast to the low irradiance treatment where the concentration remains stable compared to initial values. In *D. anceps*, on the other hand, pigment concentrations decreased under both treatments compared to initial values, especially under high irradiance (chl *a* concentrations near to 0 µg/100 µL; Fig. 6).

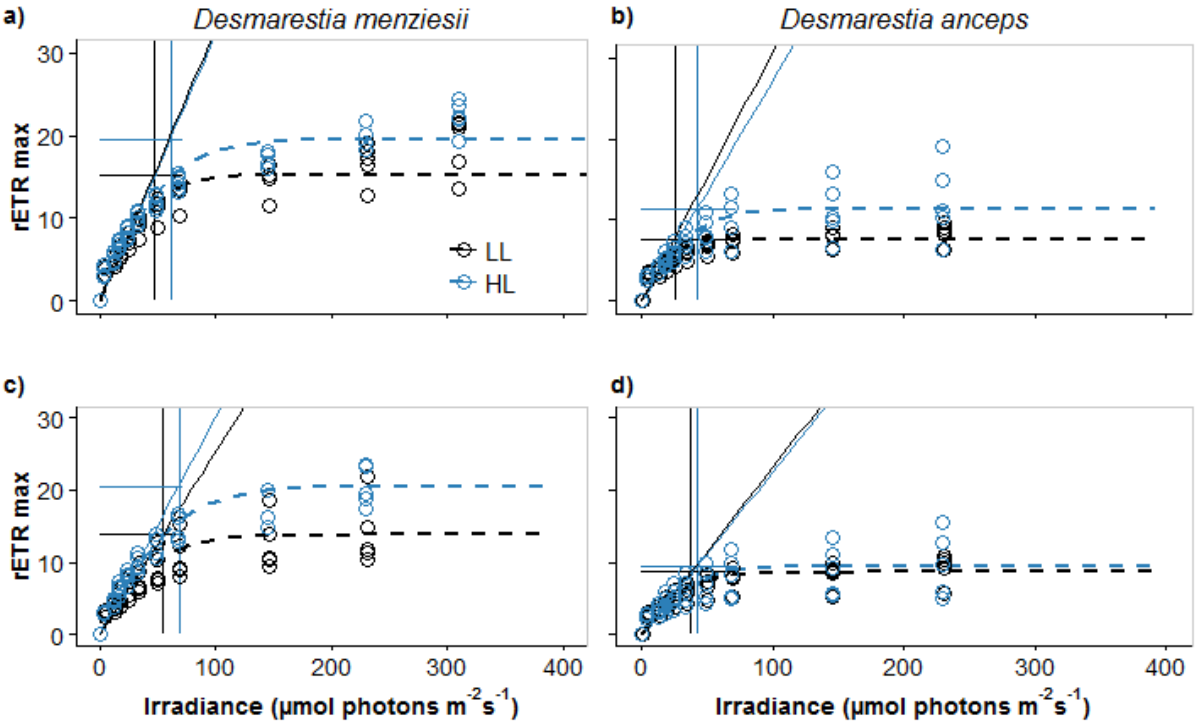


Fig.5 Maximum relative electron transport rate ($rETR_{max}$), electron transport efficiency (α), and saturation irradiance for electron transport (E_k) of mono- and co-cultured *Desmarestia menziesii* (a and c) and mono- and co-cultured *D. anceps* (b and d) under low (LL, 10 µmol m^{-2} s^{-1}) and high irradiance (HL, 100 µmol m^{-2} s^{-1}) in black and blue respectively. Curves fitted with the hyperbolic tangent model (Jassby and Platt 1976).

Table 4. One-way ANOVA of the photosynthetic efficiency parameters ($rETR_{max}$, α and E_k) of *Desmarestia menziesii* and *D. anceps* mono-cultured on culture effect (mono/co-cultures). *n*=4. p-values were set to <0.05. LI=low irradiance, HI=high irradiance, SP=species, ns = not significant. Significant values in italics.

Species	Treatment	Parameter	Source of variation	Photosynthetic efficiency		
				df	F-value	p-value
D. menziesii + *D. anceps*	LI	$rETR_{max}$	SP	1	37.5243	*0.0003*
		α		1	0.9908	ns
		E_k		1	8.7186	*0.0183*
	HI	$rETR_{max}$	SP	1	9.4480	*0.0153*
		α		1	2.9470	ns
		E_k		1	3.1112	ns

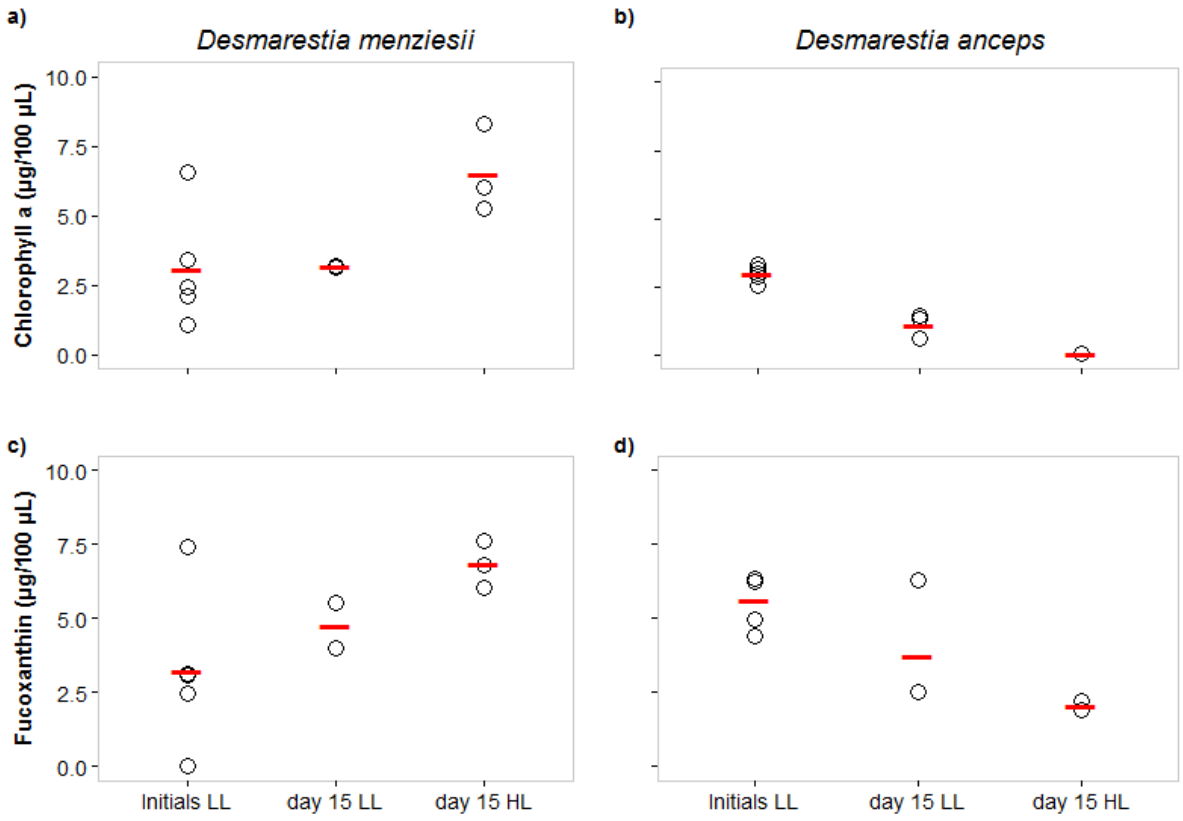


Fig.6 Chlorophyll *a* (a and b) and fucoxanthin (c and d) concentration (µg/100 µl) in *Desmarestia menziesii* and *D. anceps* specimens before and after 15 days of treatment under low irradiance (LL, 10 µmol m^{-2} s^{-1}) and high irradiance (HL, 100 µmol m^{-2} s^{-1}). Initial values refer to day 0, from specimens exposed to low irradiance. Each empty dot represent one value (Initials n=5, day 15 n=2 or 3). The red line represents the mean of the data points for each treatment.

Experiment 3. Impact of interspecific competition and temperature on D. menziesii and D. anceps

Measurements of wet weight (WW) of pre-experimental material (day -2) of both *Desmarestia* species were similar (1.14±0.06 g; one-way ANOVA, F=0.19, p=0.67). Biomass and overall growth rate was very low for both *D. menziesii* and *D. anceps* (0.44±0.22 % d^{-1} and 0.59±0.55 % d^{-1} for mono- and co-cultured *D. menziesii*; 0.58±0.45 % d^{-1} and 0.46±0.29% d^{-1} for mono- and co-cultured *D. anceps;* biomass showed in Annex 5; Fig.7) and was not significantly altered by temperature (two-way ANOVA, F=1.81, p=0.20 for *D. menziesii*; F=0.87, p=0.36 for *D. anceps*) or culture treatment (two-way ANOVA, F=0.72, p=0.41 for *D. menziesii*; F=0.93, p=0.76 for *D. anceps*).

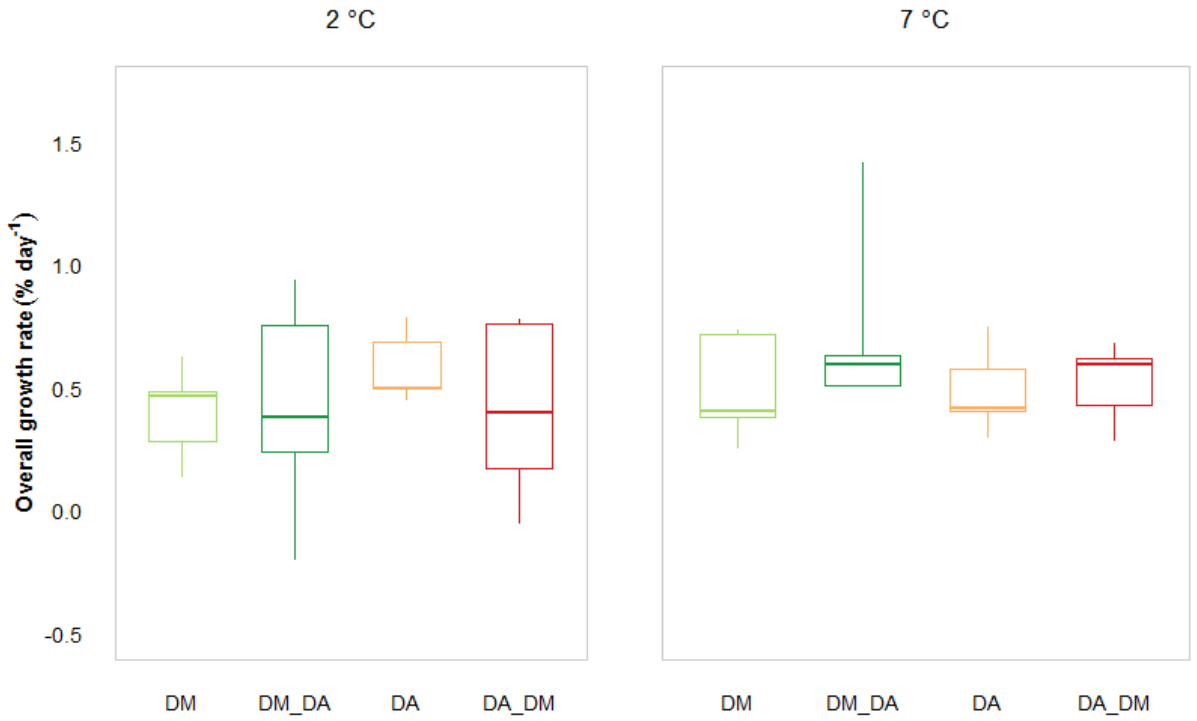


Fig.7 Box-whisker-plots of overall growth rate (% day^{-1}) of of *Desmarestia menziesii* mono-cultured (DM) and co-cultured with *D. anceps* (DM_DA), *D. anceps* mono-cultured (DA) and *D. anceps* co-cultured with *D. menziesii* (DA_DM) at 2 and 7 °C (median ± 95 to 5 percentile, n=5).

Measurements of maximum quantum yield (F_v/F_m) from pre-experimental material (day -3) were similar between both *Desmarestia* species and both temperature treatments (0.75±0.02; one-way ANOVA, F=0.71, p=0.40; Fig. 8). Generally, sporophytes of *D. menziesii* and *D. anceps* had higher maximum quantum yield at 2 compared to 7 °C (Fig. 8), but statistically significant differences were only observed for *D. anceps* (RM ANOVA, Table 5). F_v/F_m values of both *D. menziesii* and *D. anceps* showed a significant interactive effect of time and temperature treatment due to a stronger decrease in F_v/F_m at 7 °C over time compared to 2 °C (0.71±0.02 and 0.70±0.03 for *D. menziesii* and *D. anceps* at 2 °C; 0.66±0.03 and 0.65±0.03 for *D. menziesii* and *D. anceps* at 7 °C during day 10; Fig. 8; Table 5). Because both *Desmarestia* species initially showed similar F_v/F_m values, a comparison of both species after 10 days was possible (comparing mono-cultured treatments) but no difference between the two species under the two temperature treatments was detected (Table 5).

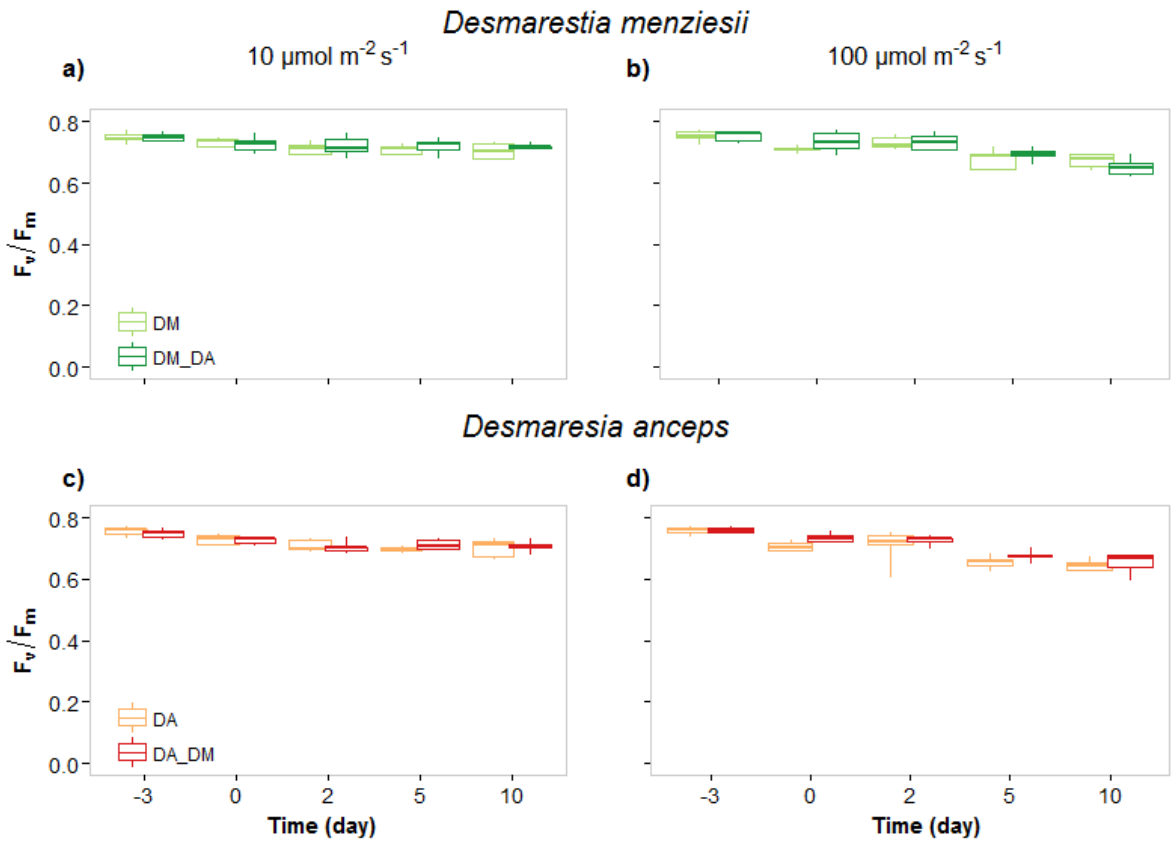


Fig.8 Box-whisker-plots of maximum quantum yield (*Fv/Fm*) of *Desmarestia menziesii* mono-cultured (DM) and co-cultured with *D. anceps* (DM_DA) (a and b), *D. anceps* mono-cultured (DA) and *D. anceps* co-cultured with *D. menziesii* (c and d) at 2°C and 7°C (median ± 95 to 5 percentile, n=5).

Almost no significant effect on the photosynthetic efficiency was detected comparing treatment effects (temperature and culture treatment) on the last sampling day. A slight interaction between temperature and culture treatment for α in *D. menziesii* was observed testing for both effects with a two-way ANOVA (F= 6.50, p= 0.02; details in Annex 7; values in Annex 6; Fig. 9). Unlike, the $rETR_{max}$ and E_k parameter of *D. menziesii* and *D. anceps* did not show any temperature or culture effects (details in Annex 7; values in Annex 6; Fig. 9). Comparing both species (mono-cultured) with each other, it became evident that only at 7 °C α parameter was lower in *D. anceps* compared to *D. menziesii* (one-way ANOVA, F= 7.9, p= 0.03; Table 6; values in Annex 6; Fig. 9).

Table 5. a) Repeated Measurements ANOVA of photosynthetic efficiency of *Desmarestia menziesii* and *D. anceps* mono- and co-cultured on temperature (2/7°C) and culture treatments (mono/co-cultures) over time (*n*=5, 10 days). b) Repeated Measurements ANOVA of maximum quantum yield (F_v/F_m) of *D. menziesii* and *D. anceps* mono-cultured on species effect (*D. menziesii*/*D. anceps*) over time (*n*=5, 10 days). TE = temperature, CU = culture treatment, TI = time, ns = not significant, *a* = variances still heterogeneous after transformation. Significant values in italics.

	Species	Source of variation	F_v/F_m		
			df	F-value	p-value
a)	*Desmarestia menziesii*	TE	1	3.74	ns
		CU	1	0.35	ns
		TE x CU	1	0.01	ns
		TI	3	21.31	*<0.0001*
		TI x TE	3	11.63	*<0.0001*
		TI x CU	3	0.57	ns
		TI x TE x CU	3	2.47	ns
	Desmarestia anceps	TE	1	12.29	*0.0029*
		CU	1	2.98	ns
		TE x CU	1	1.50	ns
		TI	3	12.40	*<0.0001*
		TI x TE	3	5.66	*0.0021*
		TI x CU	3	0.25	ns
		TI x TE x CU	3	0.57	ns
b)	*Desmarestia menziesii + Desmarestia anceps*	TE	1	12.24	*0.0030*[a]
		SP	1	4.23	ns
		TE x SP	1	1.03	ns
		TI	3	10.63	*0.0003*
		TI x TE	3	3.33	*0.0496*
		TI x SP	3	0.27	ns
		TI x TE x SP	3	0.25	ns

Initial pigment concentrations were higher for this experiment than for experiment 2 and increases or decreases were less pronounced than for experiment 2 (low vs high irradiance). Again, sporophytes of *D. menziesii* and *D. anceps* used for pigment concentration analysis were not numerically enough to be statistically analyzed. However, Fig. 10 shows a slight increase in chl *a* concentrations in *D. menziesii* after 10 days of exposure to 2 compared to 7°C were concentrations remained stable. In contrast, chl *a* concentrations in *D. anceps* decreased after 10 days under both temperatures compared to initial values, but more at 7 than at 2°C. Fucoxanthin concentrations in *D. menziesii* remained more or less stable under both temperatures compared to initial values, but they increased in *D. anceps* exposed to 2°C and decreased exposed to 7°C compared to initial values (Fig. 10).

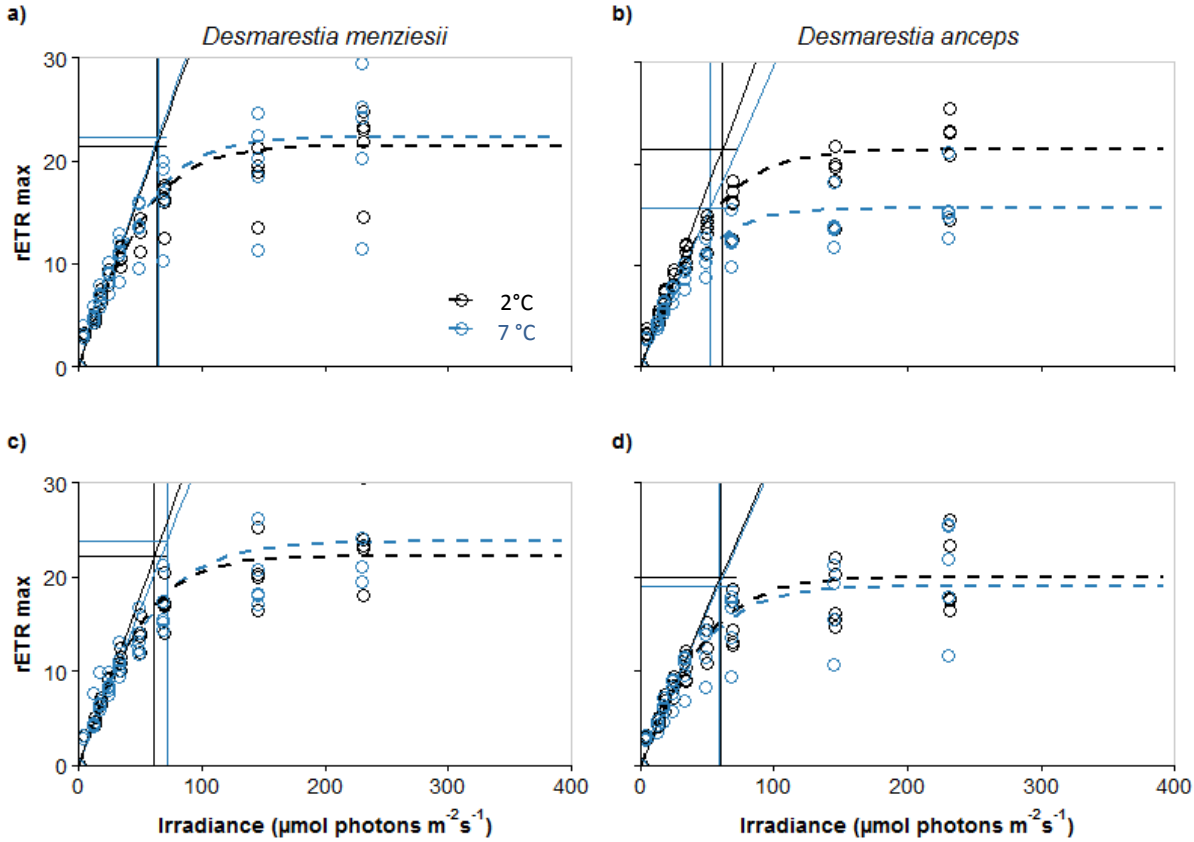


Fig.9 Maximum relative electron transport rate ($rETR_{max}$), electron transport efficiency (α), and saturation irradiance for electron transport (E_k) of mono- and co-cultured *Desmarestia menziesii* (a and c) and mono- and co-cultured *D. anceps* (b and d) under 2 °C and 7 °C in black and grey respectively.

Table 6. One-way ANOVA of the photosynthetic efficiency parameters ($rETR_{max}$, α and E_k) of *Desmarestia menziesii* and *D. anceps* mono-cultured on culture effect (mono/co-cultures). *n*=4. p-values were set to <0.05. SP=species, ns = not significant. Significant values in italics.

Species	Treatment	Parameter	Source of variation	Photosynthetic efficiency		
				df	F-value	p-value
D. menziesii + *D. anceps*	2 °C	$rETR_{max}$	SP	1	0.0138	ns
		α		1	0.728	ns
		E_k		1	0.1622	ns
	7 °C	$rETR_{max}$	SP	1	3.5324	ns
		α		1	7.9	*0.0228*
		E_k		1	1.1116	ns

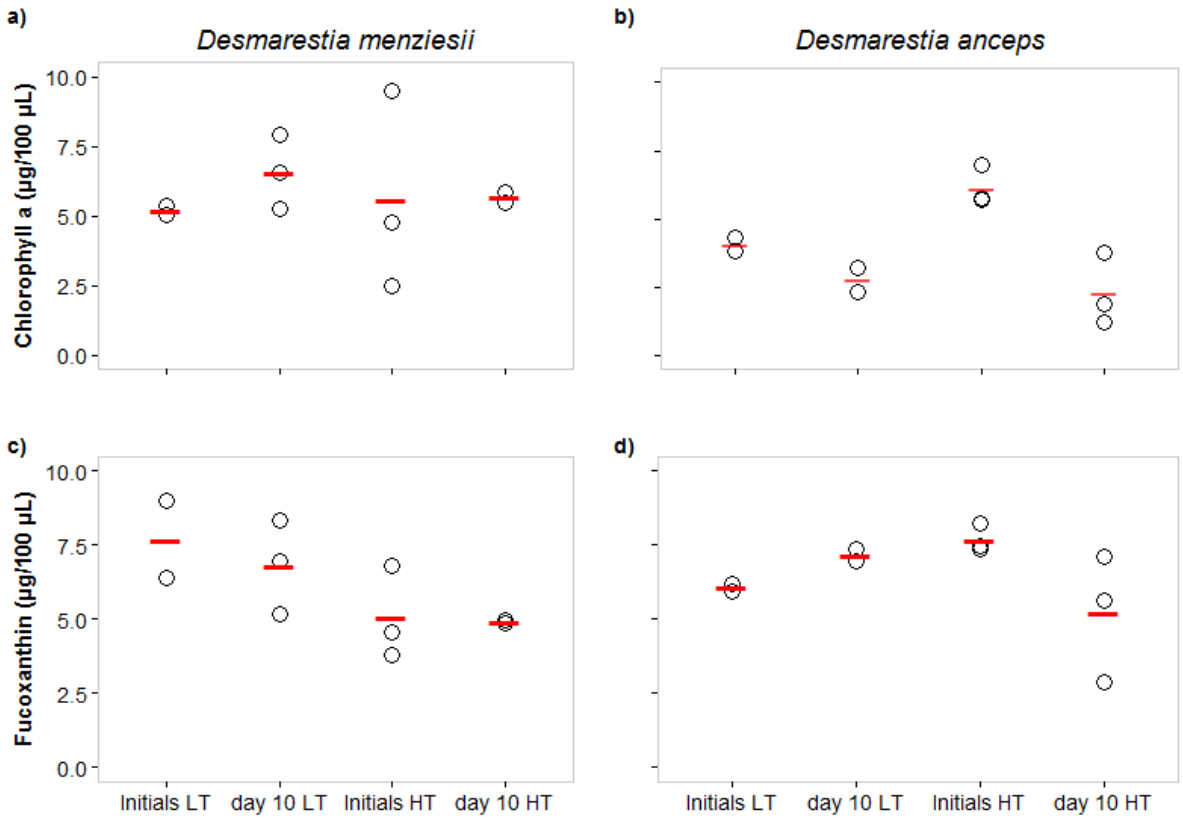


Fig.10 Chlorophyll *a* (a and b) and fucoxanthin (c and d) concentration (µg/100 µl) in *Desmarestia menziesii* and *D. anceps* specimens before and after 10 days of treatment at low temperature (LT, 2°C) and high temperature (HT, 7°C). Initial samples were taken after 2 days of exposure to the respective temperatures. Each dot represent one data (n=2 or 3). The red line represents the mean of the data points for each treatment.

IV. Discussion

This study investigated whether effects of climate change such as temperature increase and irradiance variations in the water column (due to glacier melting and therefore sediment run-off) in combination with interspecific competition may alter growth and photosynthetic performance of *Desmarestia menziesii* and *D. anceps*. These two co-occurring Antarctic brown algae did not show almost any interspecific competition effect when co-cultivated together nor when *D. menziesii* was co-cultivated with other two Antarctic red algae (*Iridaea cordata* and *Palmaria decipiens*). However, increased temperature and irradiance induced a significant stress response in both species, mostly evident on the performance of photosystem II. At 7 °C photosynthetic efficiency (F_v/F_m) decreased over time similarly in both species compared to 2 °C. Low irradiance (10 µmol m^{-2} s^{-1}) did not induce an effect on photosynthesis, but higher irradiances (50 or 100 µmol m^{-2} s^{-1}) led to a reduction of F_v/F_m at

2 °C but even more pronounced at 7 °C. The present study highlighted the key role of irradiance on the vertical distribution of these species possibly influenced by temperature.

During the current experiments, the two red algal species were growing more than the two *Desmarestia* species, and among them notably *P. decipiens* showed a very high relative growth rate (1st experiment). *Desmarestia* species grew very little at both temperatures and under both irradiance treatments, most likely because of their internal dormancy state during the summer period. *D. menziesii* and *D. anceps* are season anticipators (Kain 1989; (Wiencke 1990a; Gómez & Wiencke 1997) meaning that they start to grow under short day conditions in late winter-spring, reaching maximal growth during spring (September for *D. anceps* and December for *D. menziesii*; Wiencke 1990; Gómez & Wiencke 1997) and minimum growth activity from January to May (Wiencke 1990a). This life strategy is mainly found among the endemic Antarctic species (Lüning & tom Dieck 1989). The present experiments were carried out during the Antarctic summer (January to March), when growth of these species is minimal, which explains why no temperature or irradiance effects on the relative growth rate of *Desmarestia* spp. could be observed. In opposition, the seasonal responder *I. cordata* (Kain 1989; Weykam et al. 1997) showed a higher relative growth rate than the two brown algal species. This opportunistic life strategy is typical of the Antarctic-cold temperate species (Lüning & tom Dieck 1989) which react directly to changing environmental conditions. *Palmaria decipiens* is considered as a seasonal anticipator (Weykam et al. 1997; Lüder et al. 2002), but showed the highest relative growth rate of all tested species. However, not just season but also other factors such as age and size of the algae may influence growth rates, as has been found in other studies using temperate macroalgae (e.g. Khailov 1976). The higher relative growth rate of *P. decipiens* at 7 compared to 2 °C in this study is consistent with Wiencke & tom Dieck (1989) who observed a higher growth rate around 5 compared to 0 °C. In contrast to *P. decipiens* no temperature effects on growth were found for both *Desmarestia* species and *I. cordata.* Wiencke & tom Dieck (1989; 1990) showed optima growth rates for these species at temperatures ≤ 5 °C which could not be confirmed in this study probably due to the very low growth rates of the *Desmarestia* species in general. It is published, however, that temperatures of 10 °C can either completely stop (*D. anceps*; Wiencke & tom Dieck 1989) or reduce (*D. menziesii*, Matula & Zacher pers. comm.) their growth. The UST range of *D. anceps* is 11-12 °C (Wiencke & tom Dieck 1989) whereas the UST of *I. cordata* and *P. decipiens* is higher being between

15-16 °C and 16 – 17 °C respectively (Wiencke et al. 1994). UST of *D. menziesii* sporophytes have not been published yet, but there is evidence that it is higher than the UST of *D. anceps* (Matula & Zacher pers. comm.). This would be consistent with the biogeographic distribution of these species, with *D. menziesii* found further north up to the South Georgia Islands (54° 19' S, 36° 39' W), and of *I. cordata* found up to the southern part of Chile (Miller & Pears 1991) compared to *D. anceps* and *P. decipiens*, which only occur around the WAP up to 60° S showing lowest UST of all 4 species (Wiencke & Clayton 2002, Wiencke et al. 2014, Ricker 1987).

Under 10 µmol m^{-2} s^{-1} maximum quantum yield from *D. menziesii* and *D. anceps* remained stable over time (2nd experiment); in contrast, under 50 and 100 µmol m^{-2} s^{-1} (3rd and 2nd experiment) F_v/F_m values decreased for both species at 2 °C but even more at 7 °C (1st and 3rd experiment). Under 100 µmol m^{-2} s^{-1}, *D. menziesii* showed higher $rETR_{max}$ than under 10 µmol m^{-2} s^{-1}, meaning that after 15 days of exposure *D. menziesii* adapted to high irradiance conditions (2nd experiment). However, after 10 days of exposure to 50 µmol m^{-2} s^{-1}, the photosynthetic performance parameters of *D. menziesii* did not change at 2 and 7 °C (3rd experiment). *D. anceps* seemed to be more stressed (Maxwell and Johnson 2000) to high irradiance and high temperature conditions showing lower F_v/F_m under 50 and 100 µmol m^{-2} s^{-1} (3rd and 2nd experiments) and lower $rETR_{max}$ at 7 compared to 2 °C (3rd experiment) compared to *D. menziesii*. These results are in opposition to the outcome of Zacher et al. (2016, accepted) study, where an experiment under similar conditions (50 µmol m^{-2} s^{-1} and a day:night regime of 16:8 hours) but on cultured sporophytes of *D. menziesii* and *D. anceps* was performed. Zacher et al. (2016, accepted) showed that photosynthetic efficiency of both *Desmarestia* sp. decreased more at 0 compared to 5 °C and similarly $rETR_{max}$ of *D. menziesii* was significantly lower at 0 compared to 5 °C, indicating a sub-optimal acclimation of photosynthesis under low temperatures in combination with this irradiance conditions. Another study performed by Rautenberger et al. 2015 showed an unchanged photosynthesis of both *Desmarestia* species at 2 and 7 °C under only PAR. They could show that higher seawater temperatures decreased the UV sensitivity of *D. menziesii* whereas photosynthetic efficiency of *D. anceps* remained unaffected by combinations of temperature and UV radiation. Generally, *D. anceps* was more UV susceptible than *D. menziesii*, but it has to be considered that the experiment was performed under low irradiance conditions (18 µmol m^{-2} s^{-1}) and no consideration under enhanced irradiance intensities are taken into account.

However, they found a reduction of maximum quantum yield after UV exposure in *D. anceps* but not in *D. menziesii*, possibly a hint for the different depth zonation of both species. Generally, Antarctic endemic seaweeds are strong cold water adapted and able to perform photosynthesis at 0 °C with values as high as temperate species, but their temperature optimum for photosynthesis is above the temperature of the natural environment ranging between 5 and 15 °C (Wiencke et al. 1993, Gómez et al. 2009), which could not be confirmed with our experiments with values as high or even higher at 2 °C compared to 7 °C. However, it is known that not only sporophytes of different ages react differently to temperature but also different algal stages may react differently to environmental stressors (Coelho et al. 2000) and may have different temperature optima and USTs (reviewed in Wiencke et al. 1994). The UST of the gametophyte for example is usually higher compared to its sporophyte. The UST of the female gametophyte of *D. anceps* is with 13 °C two °C higher than of its sporophyte (Wiencke & tom Dieck 1989) and gametophytes of *D. menziesii* survive temperatures until 16-17 °C (Wiencke & tom Dieck 1990). Whether differences in algal stage or field vs. culture material are responsible for the different outcomes remains to be studied but one important fact is that most former studies were performed under low irradiance condition and high irradiance (such as used in our studies) may exert an additional stress on the algae leading to these results. In this context it is important to state that the irradiance applied during the present experiments are revealed from field data – and the algae truly experience these kinds of conditions (100 µmol m^{-2} s^{-1} at 5 m depth). This is also true for the daily PAR doses the algae may experience at 5 m which are e.g. 1130 (±500) kJ (measured in January 2014, Deregibus pers. comm.) in comparison to up to 1300 kJ applied in the 2nd experiment. Irradiance seems to be a crucial factor for the temperature tolerance of the species and it is important to use ecological relevant values. During the current experiment it was evident that the photosystem of *D. anceps* require less irradiance to saturate photosynthesis because it showed lower $rETR_{max}$ under 10 and 100 µmol m^{-2} s^{-1} (2nd experiment) compared to *D. menziesii*, highlighting that *D. anceps* is more shade-adapted compared to *D. menziesii*. The vertical distribution of these two algae explain the encountered results and it is again confirmed from the higher pigment content found in *D. menziesii* compared to *D. anceps* under high irradiance conditions. Indeed, chl *a* concentrations of *D. anceps* after 15 days of exposure time under 100 µmol m^{-2} s^{-1} reached values of almost 0 µg/100 µL suggesting the strong photodamage actualized by PSII due to

the very high irradiance intensity. *D. anceps* shows higher biomass peak at 10 m depth, where irradiance intensities are around 10 µmol m^{-2} s^{-1} once the ice has broken up, unlike *D. menziesii* which presents its higher biomass peak at 5 m depth where light intensities are normally of 100 µmol m^{-2} s^{-1}. Although *D. menziesii* shows better performance even under such high irradiance intensity, its photosynthetical activity under low irradiance did not decreased over 15 days, unlike under high irradiance. Both algae were collected where they overlap (5 m) but where a major abundance of *D. menziesii* is normally encountered (Quartino et al. 2001). Studies on photosynthetic characteristics of Antarctic macroalgae have shown that members of the *Desmarestiales* exhibit very low light requirements for saturation of photosynthesis and reach significantly higher α values than, for example, the endemic Arctic kelp *Laminaria solidungula* (Dunton and Kodwalis 1988; Wiencke et al. 1993; Kirst and Wiencke, 1995). Nevertheless, the photosynthetic efficiency (α) can be very variable according to the season. Every macroalgae species has a proper life strategy and photosynthetic parameters are life strategy – dependent. During the current experiment, the photosynthetic efficiency α shown by *D. menziesii* and *D. anceps* were particularly low (~ 0.3) which could be a consequence of the time of the year. As shown by Gomez and Wiencke (1997), α parameter of *D. menziesii* presents highest values in winter-spring and minima in summer and the photosynthesis is optimized under lower light conditions (Gomez and Wiencke, 1997). As for growth, a strong seasonal pattern of photosynthetic performance of macroalgae has been found in long-term studies (Weykam & Wiencke 1996; Weykam et al. 1997; Gómez & Wiencke 1997; Lüder et al. 2001, 2002, 2003) and in field experiments (Gutkowski & Maleszewski 1989; Drew & Hastings 1992; Gómez et al. 1995, 1997). In the brown algal season anticipators, optimal photosynthetic rates are highest in late winter (Gómez et al. 1995) or in spring as for *D. menziesii* (Gómez et al. 1997). But still there are only few studies investigating the impact of season on the temperature performance of seaweed species and none dealing with Polar species. Temperate brown algae of the order Laminariales and Desmarestiales, for example, 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* 'major effects of temperature mostly became evident during the active growth phase' (Graiff et al. 2015). These observations imply that brown algae with intermittent growth phases such as Laminariales, Fucales or Antarctic Desmarestiales (Wiencke 1990,

Gómez & Wiencke 1997) where periods of growth are followed by periods of rest over one year (Lüning & tom Dieck 1989) may exhibit seasonally different temperature affinities. This is of special interest in Antarctica where winter temperatures have been rising more than summer temperatures (Schloss et al. 2012) and the large brown Desmarestiales species have to endure a long dark winter period initiating growth during late winter by using the storage compounds build-up during spring-autumn.

No interspecific competition between *D. menziesii* and *D. anceps* (1st, 2nd and 3rd experiments) as well as between *D. menziesii* and the red algae *I. cordata* and *P. decipiens* (1st experiment) on growth was detected. Possible effects may have been masked due to the general low growth rate of the *Desmarestia* species discussed above. Interspecific competition was detected only in *D. anceps* where α was lower in co-cultured than in mono-cultured treatments under both high and low irradiance intensities (2nd experiment). Similar results were shown for *D. menziesii* with lower α values in the co-cultured compared to the mono-cultured treatments at 7 °C (3rd experiment). These results, however, were not concise over all experiments and may be an artefact. The α values give a hint on the shade adaption of a species and it is not explicable why algae co-cultured should be less shade adapted than mono-cultured. Further studies are necessary to tackle this question. The outcomes of the experiments show a general low interspecific competition between these two species. However, competition may occur in different life-cycle stages or under different environmental conditions as was pointed out by Carpenter et al. (1990). Nabivalio et al. (2014) and Xu et al. (2013), conducted experiments with different life-cycle stage (gametophytes, adult thalli) and showed both negative and positive interactions. Some species reduced the availability of resources for their competitors (resource competition; e.g. Nabivailo et al. 2014) while others influenced physiological processes of competitors via allelopathy (interference competition; Xu et al. 2013). Further studies with different developmental stages are required to find out whether in more sensitive developmental stages (e.g. spores) competition may occur and how it affects the successful colonization of both *Desmarestia* species. Competition has emerged as one of the dominant processes dictating assemblage structure (Barnes & DeGrave 2002) and especially in high latitudes is very little studied. In polar environments, glacial run-off deteriorates the underwater light climate with the potential shrink of the seasonal euphotic zone (Weslawski et al. 2011) which may lead to an increase of overlapping habitats of both species and competition in

shallower depth between species. Other factors potentially affect competition outcome and have to be known to predict the impact of climate change in such sensitive and complex environments and to understand the successful colonization of algal assemblages. Due to the decreased landfast sea-ice and increased sedimentation rates, in Arctic Kongsfjorden an altered community pattern had already been observed between 1998 and 2014 (Bartsch et al. 2016). Indeed, strong correlation between the underwater light climate and the depth distribution has been shown for both temperate and polar rocky shores (e.g. Pedersen & Snoeijs 2001, Pehlke & Bartsch 2008, Derrien-Courtel et al. 2013, Clark et al. 2015). One of the most biologically significant trends in competition was recently reported by Barnes & Neutel (2016) who revealed that the severity of competition between bryozoans (percentage of competition between colonies involved in a win/loss outcome, leading to death of the loser) was three times lower at the poles than in the tropics. Moreover, the most frequent spatial competition at the poles was found to be intraspecific unlike the non-polar regions where competition is dominated by species of different families (shift of the relatedness of competitors towards the poles). Such situation, which is not just a scenario but already evidence, leads to a simplification of the fauna and flora communities, where just few organisms outcompete the others. Therefore, it is necessary to further investigate which are the key factors which regulate competition within assemblages of Polar macroalgae as no other studies on this topic exist.

Although a temperature increase to 7 °C in summer does not seem to be mortal 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. However, experiments should take into consideration the combined effects with other factors, which may act in a synergistic or antagonistic way. Further investigations on all life cycle stages (spores, gametophytes, young and adult sporophytes), reproduction (e.g. gametogenesis) and subsequent recruitment in different seasons would be important to generate a more complete picture and to better understand the effects of increasing temperatures on species and macroalgal assemblages. The current experiments were relatively short in duration and there is a need to look at the effects of climate change parameters over both, short- and long-term exposures. However, opposite results have been detected between laboratory and field material experiments, suggesting that laboratory experiments may still be improved and care must be taken in extrapolating small scale

laboratory experiments of one developmental stage to the whole algal organism developing under field conditions. As shown by Zacher (2014) spores exposed to field and laboratory conditions germinated at significantly higher rates in the laboratory due to a lower PAR to UVR ratio applied compared to field conditions. Especially the high PAR irradiance in the field impeded germination of spores from the endemic algal species *Himantothallus grandifolius* at lower depths and seems – at least partly – responsible for the depth zonation of this species. All this shows that it is essential to take seasonal patterns into account and that working with field material *in situ* is of great importance to investigate community responses under global climate change.

References

Amsler, C. D., Rowley, R. J., Laur, D. R., Quetin, L. B., & Ross, R. M. (1995). Vertical distribution of Antarctic peninsular macroalgae: cover, biomass and species composition*. Phycologia, 34(5), 424-430.

Barnes, D. K. (2002). Polarization of competition increases with latitude. Proceedings of the Royal Society of London B: Biological Sciences, 269(1504), 2061-2069.

Barnes, D. K. A., & Neutel, A. M. (2016). Severity of seabed spatial competition decreases towards the poles. Current Biology, 26(8), R317-R318.

Bartsch, I., Wiencke, C., Bischof, K., Buchholz, C. M., Buck, B. H., Eggert, A., Feuerpfeil, P., Hanelt, D., Jacobsen, S., Karez, R., Karsten, U., Molis, M., Roleda, M. Y., Schubert, H., Schumann, R., Valentin, K., Weinberger, F. & Wiese, J. (2008): The genus Laminaria sensu lato: recent insights and developments. – Eur. J. Phycol. 43: 1–86.

Bartsch, I., Paar, M., Fredriksen, S., Schwanitz, M., Daniel, C., Hop, H., & Wiencke, C. (2016). Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming. Polar Biology, 1-16.

Brouwer, P. E. M. (1996): Decomposition in situ of the sublittoral Antarctic macroalga Desmarestia anceps Montagne. – Polar Biol. 16: 129–137.

Carpenter, R.C. (1990): Competition among marine macroalgae: a physiological perspective. – J. Phycol. 26: 6–12.

Chung, H., Oh, Y. S., Lee, I. K., & Kim, D. Y. (1994). Macroalgal vegetation of Maxwell Bay in King George Island, Antarctica. Korean J. Phycol, 9, 47-58.

Clark, G. F., Marzinelli, E. M., Fogwill, C. J., Turney, C. S., & Johnston, E. L. (2015). Effects of sea-ice cover on marine benthic communities: a natural experiment in Commonwealth Bay, East Antarctica. Polar Biology, 38(8), 1213-1222.

Clarke, A., Murphy, E. J., Meredith, M. P., King, J. C., Peck, L. S., Barnes, D. K., & Smith, R. C. (2007). Climate change and the marine ecosystem of the western Antarctic Peninsula. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 362(1477), 149-166.

Clayton, M. N. (1994): Evolution of the Antarctic marine benthic algal flora. – J. Phycol. 30: 897–904.

Coelho, S. M., Rijstenbil, J.W. & Brown, M. T. (2000): Impacts of anthropogenic stresses on the early development stages of seaweeds. – J. Aquat. Ecosys. Stress Recov. 7: 317–333.

DeLaca, T. E., & Lipps, J. H. (1976). Shallow-water marine associations, Antarctic Peninsula. Antarct J US, 11(1), 12-20.

Deregibus, D., Quartino, M. L., Campana, G. L., Momo, F. R., Wiencke, C., & Zacher, K. (2016). Photosynthetic light requirements and vertical distribution of macroalgae in newly ice-free areas in Potter Cove, South Shetland Islands, Antarctica. Polar Biology, 39(1), 153-166.

Deregibus, D., Scharf, F. K., Pasotti, F., Ruiz B. E., Servetto, N., Abele, D. (2015): IMCONet Research Areas Map of Potter Cove, King-George Island (I. 25 de Mayo), with links to maps. Instituto Antártico Argentino, Buenos Aires, Argentina, doi:10.1594/PANGAEA.853859

Derrien-Courtel, S., Le Gal, A., & Grall, J. (2013). Regional-scale analysis of subtidal rocky shore community. Helgoland Marine Research, 67(4), 697-712.

Drew, E. A., & Hastings, R. M. (1992). A year-round ecophysiological study of Himantothallus grandifolius (Desmarestiales, Phaeophyta) at Signy Island, Antarctica. Phycologia, 31(3-4), 262-277.

Ducklow, H. W., Fraser, W. R., Meredtih, M. P., Stammerjohn, S. E., Doney, S. C., Martinson, D. G., Sailley, S. F., Schofield, O. M., Steinberg, D. K., Venables, H., J., Amsler, C. D. (2013) West Antarctic Peninsula: an ice-dependent coastal marine ecosystem in transition. Oceanography 26:190–203

Dunton, K. H., & Jodwalis, C. M. (1988). Photosynthetic performance of Laminaria solidungula measured in situ in the Alaskan High Arctic. Marine Biology, 98(2), 277-285.

Gómez, I. & Wiencke, C. (1996): Seasonal growth and photosynthetic performance of the Antarctic macroalga Desmarestia menziesii (Phaeophyceae) cultivated under fluctuating Antarctic daylengths. – Bot. Mar. 110: 25–31.

Gömez, I., & Wiencke, C. (1997). Seasonal growth and photosynthetic performance of the Antarctic macroalga Desmarestia menziesii (Phaeophyceae) cultivated under fluctuating Antarctic daylengths. Botanica Acta, 110(1), 25-31.

Gómez, I., Wiencke, C., & Weykam, G. (1995). Seasonal photosynthetic characteristics of ----- Ascoseira mirabilis (Ascoseirales, Phaeophyceae) from King George Island, Antarctica. Marine Biology, 123(1), 167-172.

Gómez, I., Wulff, A., Roleda, M. Y., Huovinen, P., Karsten, U., Quartino, M. L., Dunton, K. & Wiencke, C. (2009): Light and temperature demands of marine benthic microalgae and seaweeds in polar regions. – Bot. Mar. 52: 593–608.

Graiff, A., Liesner, D., Karsten, U. & Bartsch, I. (2015): Temperature tolerance of western Baltic Sea Fucus vesiculosus – growth, photosynthesis and survival. – J. Exp. Mar. Biol. Ecol. 471: 8–16.

Gutkowski, R. & Maleszewski, S. (1989). Seasonal changes of the photosynthetic capacity of the Antarctic macroalga Adenocystis utricularis (Bory) Skottsberg. Polar Biology, 10(2), 145-148.

Henley, W. J. (1993). Measurement and interpretation of photosynthetic light-response curves in algae in the context of photoinhibition and diel changes. Journal of Phycology, 29(6), 729-739.

Huang Y. M., Amsler, M. O., McClintock, J. B., Amsler, C. D. & Baker B. J. (2007): Patterns of gammarid amphipod abundance and species composition associated with dominant subtidal macroalgae along the western Antarctic Peninsula. – Polar Biol. 30: 1417–1430.

IPCC (2013) Summary for Policymakers. In: Stocker, T. F., Qin, D., Plattner, G-K, Tignor, M., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.,M. (eds) Climate change 2013: the physical science basis contribution of working group i to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York

Jassby, A. D. & Platt, T. (1976): Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. – Limnol. Oceanogr. 21: 540–547.

Kain, J. M. (1989). The seasons in the subtidal. British Phycological Journal, 24(3), 203-215.

Khailov, K. M. (1976). The relationships between weight, length, age and intensity of photosynthesis and organotrophy of macrophytes in the Barents Sea. Botanica Marina, 19(6), 335-340.

Kirst, G. O., & Wiencke, C. (1995). Ecophysiology of polar algae. Journal of Phycology, 31(2), 181-199.

Klöser H., Quartino M. L. & Wiencke C. (1996). Distribution of macroalgae and macroalgal communities in gradients of physical conditions in Potter Cove, King George Island, Antarctica. Hydrobiologia, 333(1), 1-17.

Klöser, H., Ferreyra, G., Schloss, I., Mercuri, G., Laturnus, F. & Curtosi, A. (1993). Seasonal variation of algal growth conditions in sheltered Antarctic bays: the example of Potter Cove (King George Island, South Shetlands). Journal of Marine Systems, 4(4), 289-301.

Lüder, U. H., Knoetzel, J. & Wiencke, C. (2002). Acclimation of photosynthesis and pigments to seasonally changing light conditions in the endemic Antarctic red macroalga *Palmaria decipiens* (pp. 231-236). Springer Berlin Heidelberg.

Lüder, U. (2003). Acclimation of the photosynthetic apparatus of the endemic Antarctic red macroalga Palmaria decipiens to seasonally changing light conditions= Akklimatisation des Photosyntheseapparates der endemisch antarktischen roten Makroalge *Palmaria decipiens* an saisonal wechselnde Lichtbedingungen. Berichte zur Polar-und Meeresforschung (Reports on Polar and Marine Research), 469

Lüder, U. H., Wiencke, C., & Knoetzel, J. (2002). Acclimation of photosynthesis and pigments during and after six months of darkness in Palmaria decipiens (rhodophyta): a study to simulate Antarctic winter sea ice cover. Journal of phycology, 38(5), 904-913.

Lüning, K. (1990): Seaweeds: their environment, biogeography and ecophysiology. John Wiley & Sons, New York, 531 pp.

Lüning, K. & tom Dieck, I. (1989). Environmental triggers in algal seasonality. Botanica Marina, 32, 389-397.

Miller, K. A., & Pearse, J. S. (1991). Ecological studies of seaweeds in McMurdo Sound, Antarctica. American Zoologist, 31(1), 35-48.

Müller, R., Wiencke, C., Bischof, K. & Krock, B. (2009): Zoospores of three Arctic Laminariales under different UV radiation and temperature conditions: exceptional spectral absorbance properties and lack of phlorotannin induction. – Photochem. Photobiol. 85: 970–977.

Nabivailo, Y. V. & Titlyanov, E. A. (2006): Competitive relationships in natural and artificial algal communities. – Russ. J. Mar. Biol. 32: 21–31.

Nabivailo, Y. V., Skriptsova, A. V. & Titlyanov E. A. (2014): The interspecific relationships of seaweeds and their role in the formation of communities of Ahnfeltia tobuchiensis (Kanno et Matsubara, 1932) Makienko, 1970 (Rhodophyta). – Russ. J. Mar. Biol. 40: 344–353.

Olson, A., M. & Lubchenco, J. (1990): Competition in seaweeds: Linking plant traits to competitive outcomes. – J. Phycol. 26: 1–6.

Paar, M., Voronkov, A., Hop, H., Brey, T., Bartsch, I., Schwanitz, M., Wiencke, C., Lebreton, B. & Asmus, H. (2015). Temporal shift in biomass and production of macrozoobenthos in the macroalgal belt at Hansneset, Kongsfjorden, after 15 years. Polar Biology, 1-12.

Pedersen, M. & Snoeijs, P. (2001). Patterns of macroalgal diversity, community composition and long-term changes along the Swedish west coast. Hydrobiologia, 459(1-3), 83-102.

Pehlke, C. & Bartsch, I. (2008). Changes in depth distribution and biomass of sublittoral seaweeds at Helgoland (North Sea) between 1970 and 2005. Climate Research 37, 135-147.

Provasoli, L., 1968. Media and prospects for the cultivation of marine algae. In A. Watanabe & A. Hattori (eds), Cultures and Collections of Algae. Jap. Society of Plant Physiol.: 63–75.

Quartino, M. L. & De Zaixso, A., B. (2008): Summer macroalgal biomass in Potter Cove, South Shetland Islands, Antarctica: its production and flux to the ecosystem. – Polar Biol. 31: 281–294.

Quartino, M. L., Klöser, H., Schloss, I. & Wiencke, C. (2001): Biomass and associations of benthic marine macroalgae from the inner Potter Cove (King George Island, Antarctica) related to depth and substrate. – Polar Biol. 24: 349–355.

Reed, D. C. (1990): The effects of variable settlement and early competition on pattern of kelp recruitment. – Ecology 71: 776–787.

Reichardt, W. (1987): Burial of Antarctic macro algal debris in bioturbated deep-sea sediments. – Deep-Sea Res. 34: 1761–1770.

Ricker, R. W. (1987). Taxonomy and biogeography of Macquarie Island seaweeds. British Museum (Natural History).

Roleda, M. Y. Hanelt, D. & Wiencke, C. (2006): Exposure to ultraviolet radiation delays photosynthetic recovery in Arctic kelp zoospores. – Photosyn. Res. 88(3): 311-322

Schloss, I. R., Abele, D., Moreau, S., Demers, S., Bers, A. V., González, O. & Ferreyra, G. A. (2012): Response of phytoplankton dynamics to 19-year (1991–2009) climate trends in Potter Cove (Antarctica). – J. Marine Syst. 92: 53–66.

Schloss I. R., Ferreyra, G., A. & Ruiz-Pino D. (2002): Phytoplankton biomass in Antarctic shelf zones: a conceptual model based on Potter Cove, King George Island. – J. Marine Syst. 36: 129–143.

Schloss, I. R., & Ferreyra, G. A. (2002). Primary production, light and vertical mixing in Potter Cove, a shallow bay in the maritime Antarctic (pp. 117-124). Springer Berlin Heidelberg.

Shea, R., & Chopin, T. (2007). Effects of germanium dioxide, an inhibitor of diatom growth, on the microscopic laboratory cultivation stage of the kelp, Laminaria saccharina. Journal of Applied Phycology, 19(1), 27-32.

Turley C. (2013) Ocean acidification. In: Noone KJ, Sumaila UR, Diaz RJ (eds) Managing ocean environments in changing climate: sustainability and economic perspectives. Elsevier, Amsterdam, pp 15–44

Turner J. & Overland J. (2009a): Contrasting climate change in the two polar regions. – Polar Res. 28: 146–164.

Turner, J., Bindschadler, R., Convey, P., Di Prisco, G., Fahrbach, E., Gutt, J., Hodgson, D., Mayewski, P., Summerhayes, C. (Eds.) (2009b). Antarctic Climate Change and the Environment. Scientific Commettee on Antarctic Research, Cambridge.

Węsławski, J. M., Kendall, M. A., Włodarska-Kowalczuk, M., Iken, K., Kędra, M., Legezynska, J., & Sejr, M. K. (2011). Climate change effects on Arctic fjord and coastal macrobenthic diversity observations and predictions. Marine Biodiversity, 41(1), 71-85.

Weykam, G., & Wiencke, C. (1992). Seasonal photosynthetic performance of the endemic Antarctic alga Palmaria decipiens (Reinsch) Ricker. Plant Physiol (Life Sci Adv), 11, 225-232.

Weykam, G., Thomas, D. N., & Wiencke, C. (1997). Growth and photosynthesis of the Antarctic red algae Palmaria decipiens (Palmariales) and Iridaea cordata (Gigartinales) during and following extended periods of darkness. Phycologia, 36(5), 395-405.

Wiencke, C., Amsler, C. D. & Clayton, M. N. (2014): Macroalgae. – In: De Broyer, C., Koubbi, P., Griffiths, H.J., Raymond, B. & Udekem d'Acoz, C. d' et al. (eds.), Biogeographic atlas of the Southern Ocean. Scientific Committee on the Antarctic Research. Cambridge, pp. 66–73.

Wiencke, C. & tom Dieck, I. (1989): Temperature requirements for growth and temperature tolerance of macroalgae endemic to the Antarctic region. – Mar. Ecol. Prog. Ser. 54: 189–197.

Wiencke, C. (1990a). Seasonality of brown macroalgae from Antarctica—a long-term culture study under fluctuating Antarctic daylengths. Polar Biology, 10(8), 589-600.

Wiencke, C. (1990b). Seasonality of red and green macroalgae from Antarctica—a long-term culture study under fluctuating Antarctic daylengths. Polar Biology, 10(8), 601-607.

Wiencke, C., Bartsch, I., Bischoff, B., Peters A.F. & Breeman A.M. (1994): Temperature requirements and biogeography of Antarctic, Arctic and amphiequatorial seaweeds. – Bot. Mar. 37: 247–259.

Wiencke, C., Clayton, M.N., Gómez, I., Iken, K., Lüder, U., Amsler, C.D., Karsten, U., Hanelt, D., Bischof, B. & Dunton, K. (2007): Life strategy, ecophysiology and ecology of seaweeds in polar waters. – Rev. Environ. Sci. Biotech. 6: 95–126.

Wiencke, C., Ferreyra, G. A., Abele, D., & Marenssi, S. (2008). The Antarctic ecosystem of Potter cove, King-George Island (Isla 25 de Mayo): Synopsis of research performed 1999-2006 at the Dallmann Laboratory and Jubany Station.Berichte zur Polar-und Meeresforschung (Reports on Polar and Marine Research), 571.

Wiencke, C., Gómez, I., & Dunton, K. (2009). Phenology and seasonal physiological performance of polar seaweeds. Botanica Marina, 52(6), 585-592.

Wiencke, C., Roleda, M. Y., Gruber, A., Clayton, M. N., & Bischof, K. (2006). Susceptibility of zoospores to UV radiation determines upper depth distribution limit of Arctic kelps: evidence through field experiments. Journal of Ecology, 94(2), 455-463.

Wiencke, C., tom Dieck, I. (1989). Temperature requirements for growth and temperature tolerance of macroalgae endemic to the Antarctic region. Mar Ecol Prog Ser 54:189-197

Xu D., Li F., Gao Z., Wang D., Zhang X., Ye N. & Zhuang Z. (2013): Facilitative interactions between the green-tide macroalga Monostroma arctium and the red macroalga Porphyra yezoensis. – J. Exp. Mar. Biol. Ecol. 444: 8–15.

Zacher K., Savaglia V., Bartsch I. (2016, accepted): Effects of temperature and interspecific competition on growth and photosynthesis of two endemic Antarctic Desmarestia species. Algological studies

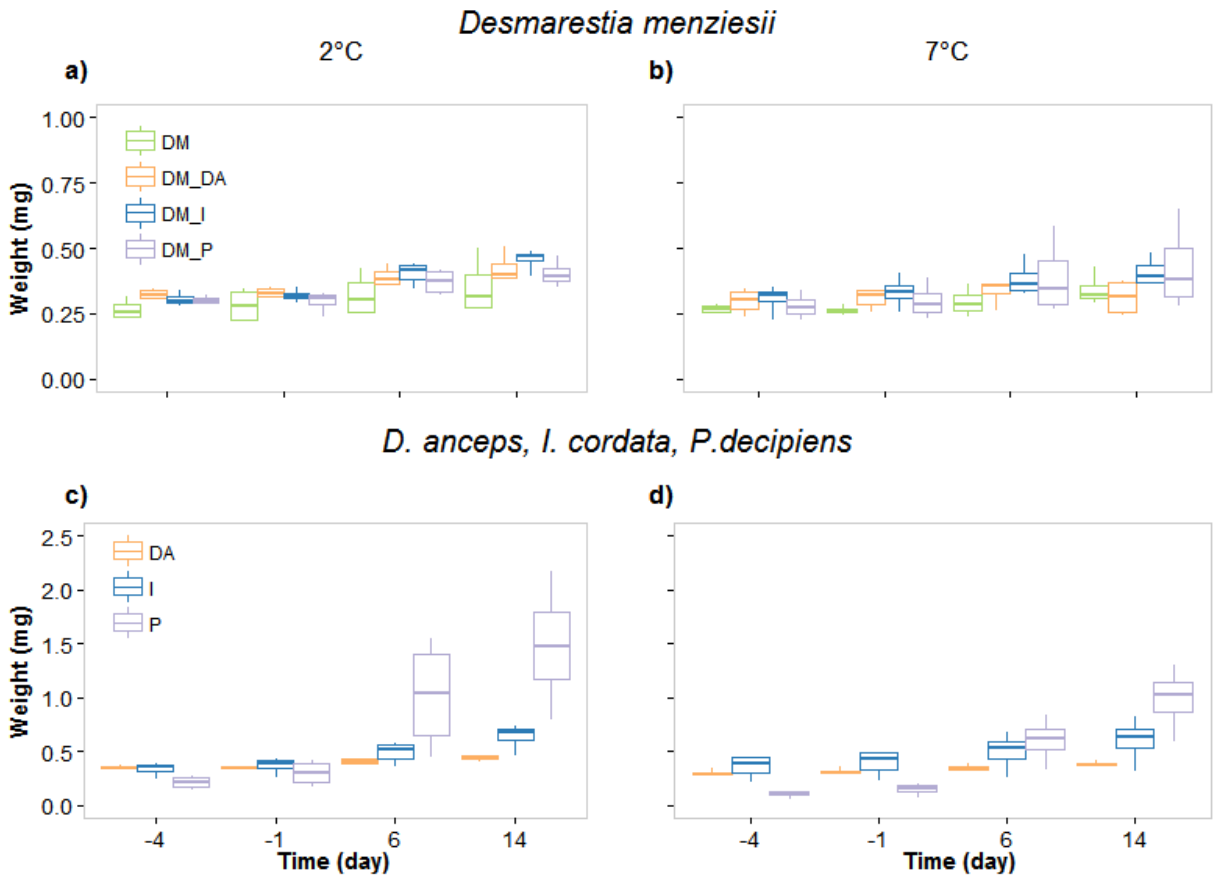
Zacher, K. (2007). Effects of uv radiation on Antarctic benthic algae-with emphasis on early successional stages and communities= Effekte von UV-Strahlung auf antarktische benthische Algen-mit Schwerpunkt auf jungen Entwicklungsstadien und Gemeinschaften. Berichte zur Polar- und Meeresforschung (Reports on Polar and Marine Research), 567.

Zacher, K. (2014): The susceptibility of spores and propagules of Antarctic seaweeds to UV and photosynthetically active radiation – Field versus laboratory experiments. – J. Exp. Mar. Biol. Ecol. 458: 57–63.

ANNEX

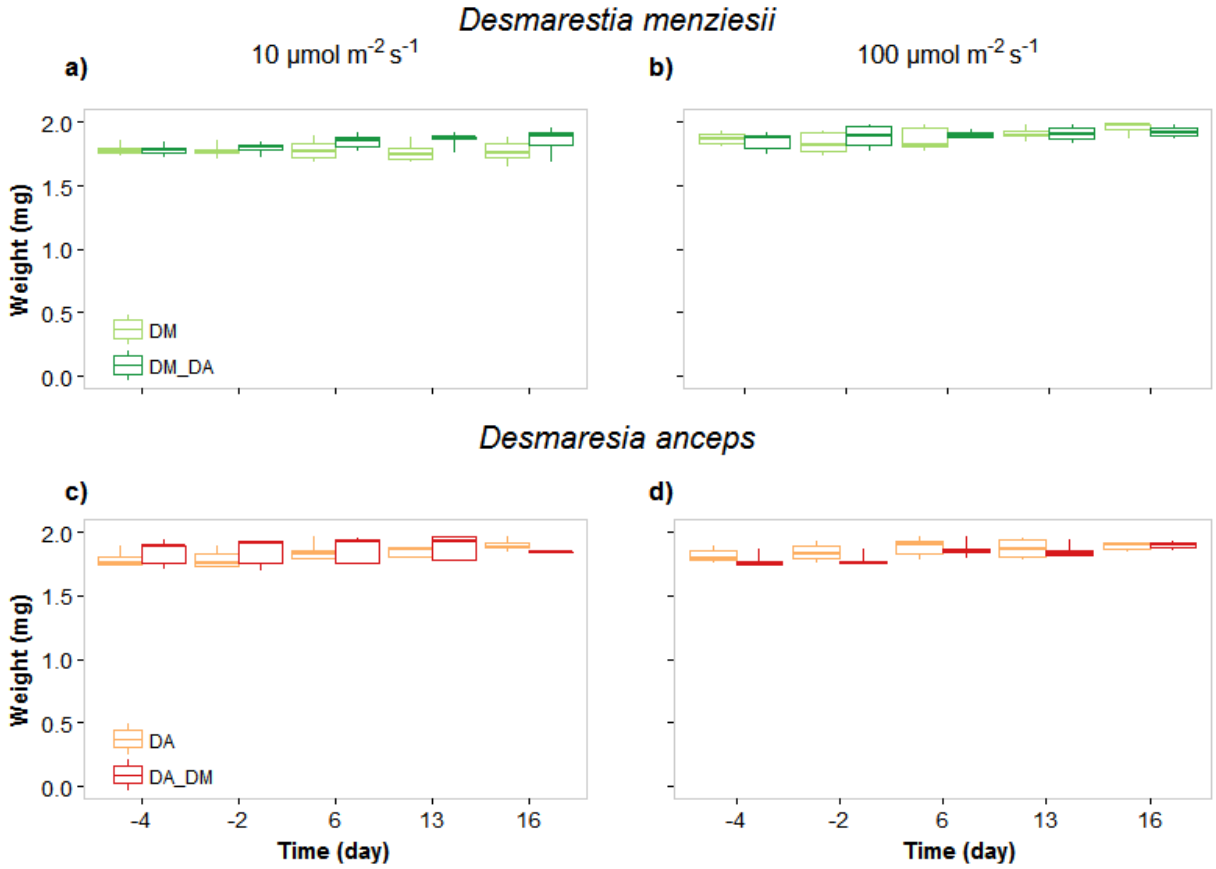
Experiment 1. Impact of interspecific competition and temperature on D. menziesii

Annex 1. Box-whisker-boxplot of biomass (weight, mg) of *Desmarestia menziesii* mono-cultured (DM) and co-cultured with *D. anceps* (DM_DA), *I. cordata* (DM_I), *P. decipiens* (DM_P) and *D. anceps* (DA), *I. cordata* (I) and *P. decipiens* (P) co-cultured with *D. menziesii* at 2°C and 7 °C (median ± 95 to 5 percentile, n=4).



Experiment 2. Impact of interspecific competition and irradiance on D. menziesii and D. anceps

Annex 2. Box-whisker-boxplot of biomass (weight, mg) of *Desmarestia menziesii* mono-cultured (DM) and co-cultured with *D. anceps* (DM_DA) (a and b), *D. anceps* mono-cultured (DA) and *D. anceps* co-cultured with *D. menziesii* (DA_DM) (c and d) under 10 and 100 µmol m^{-2} s^{-1} (median ± 95 to 5 percentile, n=5).



Annex 3. Maximum relative electron transport rate ($rETR_{max}$), electron transport efficiency (α), and saturation irradiance for electron transport (E_k) derived from rapid light curves and calculated by the hyperbolic tangent model (Jassby & Platt 1976) of *Desmarestia menziesii* and *D. anceps* during the first experimental day (initial, day 0) and after 15 days of exposure to low (LI, 10 µmol m^{-2} s^{-1}) and high irradiance (HI, 100 µmol m^{-2} s^{-1}) (means ± SD, n=5).

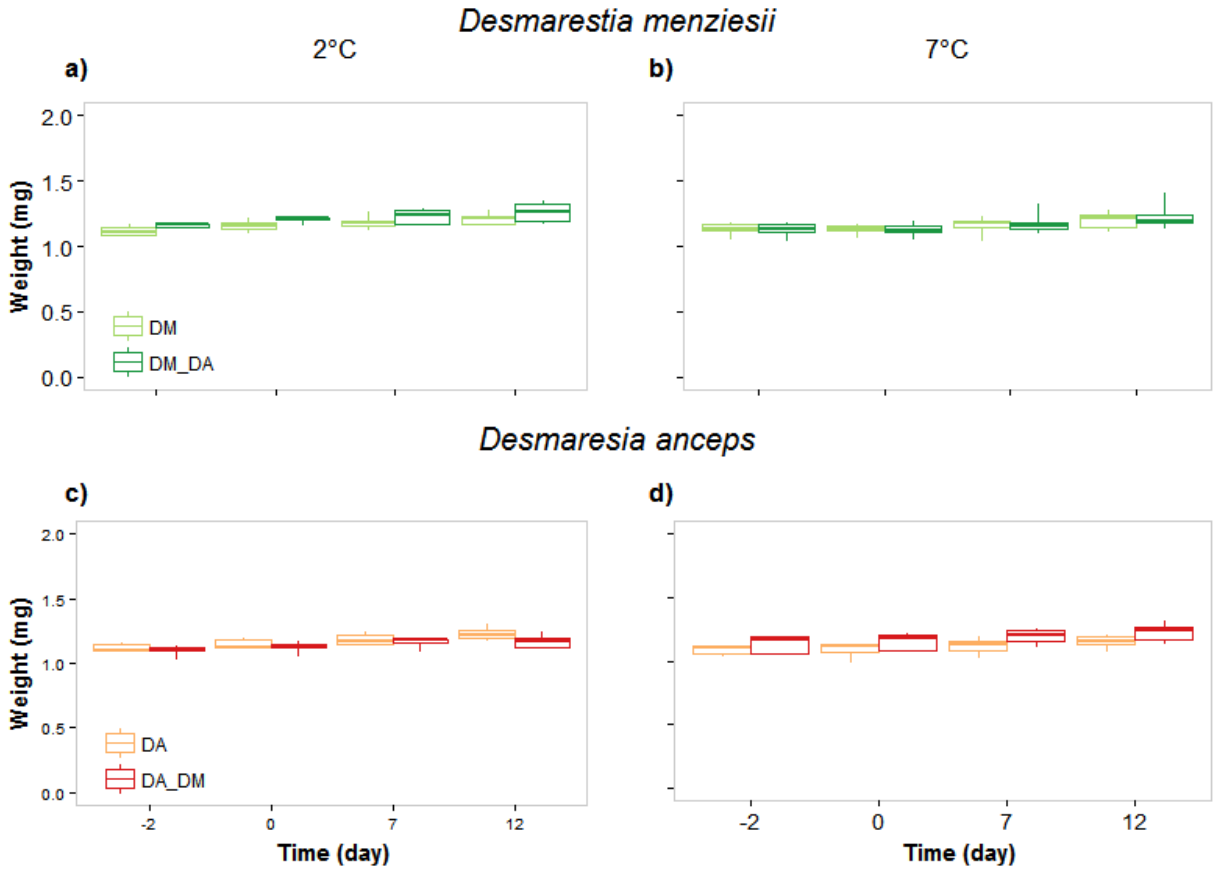
	mono-cultured				co-cultured			
	LI		HI		LI		HI	
	Initial	Day 15	Initial	Day 15	Initial	Day 15	Initial	Day 15
Desmarestia menziesii								
$rETR_{max}$	16.81 ± 2.345	16.99 ±2.15	19.35 ± 2.15	18.978 ± 1.4	14.56 ± 3.52	13.81 ± 4.80	16.99 ± 2.15	20.58 ± 2.89
alpha	0.36 ± 0.08	0.30 ±0.04	0.31 ± 0.00	0.31 ± 0.02	0.32 ± 0.06	0.25 ± 0.05	0.30 ± 0.04	0.30 ± 0.03
E_k	47.65 ± 9.99	56.36 ± 7.76	62.31 ± 7.01	60.52 ± 6.22	48.00 ± 17.63	53.44 ± 10.36	56.36 ± 7.76	68.36 ± 4.91
Desmarestia anceps								
$rETR_{max}$	11.74 ± 3.69	7.83 ±1.14	14.26 ± 3.59	11.89 ± 4.30	11.16 ±4.28	8.47± 1.88	12.61± 5.26	9.53 ± 4.33
α	0.31 ± 0.05	0.30 ± 0.03	0.30 ± 0.06	0.28 ± 0.03	0.33 ± 0.08	0.28 ± 0.03	0.28 ± 0.06	0.24 ± 0.05
E_k	39.12 ± 14.64	26.31± 3.08	49.29 ± 14.69	42.85 ± 15.64	36.23 ± 18.04	35.40± 6.75	46.97 ± 26.05	35.56 ± 13.59

Annex 4. Two-way ANOVA of the photosynthetic efficiency parameters ($rETR_{max}$, α and E_k) of *Desmarestia menziesii* and *D. anceps* on irradiance (10/100 µmol m^{-2} s^{-1}) and culture treatments (mono/co-cultures). *n*=4. p-values were set to <0.05. IR = irradiance, CU = culture treatment, ns = not significant. Significant values in italics.

Species	Parameter	Source of variation	Photosynthetic efficiency		
			df	F-value	p-value
Desmarestia menziesii	$rETR_{max}$	IR	1	6.1105	*0.0250*
		CU	1	0.2365	ns
		IR x CU	1	0.0375	ns
	α	IR	1	0.0571	ns
		CU	1	1.0835	ns
		IR x CU	1	0.0007	ns
	E_k	IR	1	2.6297	ns
		CU	1	0.0871	ns
		IR x CU	1	0.0198	ns
Desmarestia anceps	$rETR_{max}$	IR	1	3.1152	ns
		CU	1	0.3501	ns
		IR x CU	1	1.0663	ns
	α	IR	1	0.2340	ns
		CU	1	9.2820	*0.0077*
		IR x CU	1	0.2600	ns
	E_k	IR	1	2.8836	ns
		CU	1	0.0340	ns
		IR x CU	1	2.7677	ns

Experiment 3. Impact of interspecific competition and temperature on D. menziesii and D. anceps

Annex 5. Box-whisker-plots of biomass (weight, mg) of *Desmaresti menziesii* mono-cultured (DM) and co-cultured with *D. anceps* (DM_DA), *D. anceps* mono-cultured (DA) and *D. anceps* co-cultured with *D. menziesii* at 2 (a) and 7 °C (b) (median ± 95 to 5 percentile, n=5).



Annex 6. Maximum relative electron transport rate ($rETR_{max}$), electron transport efficiency (α), and saturation irradiance for electron transport (E_k) derived from rapid light curves and calculated by the hyperbolic tangent model (Jassby & Platt 1976) of *Desmarestia menziesii* and *D. anceps* during the first experimental day (initial, day 0) and after 10 days of exposure to low (2°C) and high temperature (7°C) (means ± SD, n=5).

	mono-cultured				co-cultured			
Mean ± SD	2 °C Initial	2 °C Day 10	7 °C Initial	7 °C Day 10	2 °C Initial	2 °C Day 10	7 °C Initial	7 °C Day 10
Desmarestia menziesii								
$rETR_{max}$	26.5 ± 2.76	23.8 ± 0.92	28.1 ± 4.79	25.6 ± 5.49	20.9 ± 7.80	24.0 ± 7.69	20.1 ± 2.94	21.7 ± 2.60
α	0.37 ± 0.02	0.33 ± 0.03	0.35 ± 0.01	0.38 ± 0.03	0.32 ± 0.01	0.35 ± 0.03	0.34 ± 0.03	0.31 ± 0.02
E_k	71.9 ± 9.16	71.5 ± 6.08	64.5 ± 23.7	68.4 ± 17.5	64.5 ± 23.7	67.9 ± 22.3	59.2 ± 10.3	69.4 ± 3.91
Desmarestia anceps								
$rETR_{max}$	23.1 ± 4.94	24.0 ± 1.60	14.1 ± 1.62	15.6 ± 3.42	18.8 ± 3.41	22.9 ± 4.45	17.7 ± 3.59	20.0 ± 5.63
α	0.37 ± 0.04	0.35 ±0.04	0.36 ± 0.02	0.30 ± 0.03	0.34 ± 0.04	0.33 ± 0.04	0.34 ± 0.02	0.32 ± 0.05
E_k	62.2 ± 9.35	69.3 ± 9.44	49.8 ± 3.46	52.0 ± 10.5	62.8 ± 9.41	59.7 ± 9.63	53.0 ± 12.7	61.9 ± 10.9

Annex 7. Two-way ANOVA of the photosynthetic efficiency parameters ($rETR_{max}$, α and E_k) of *Desmarestia menziesii* and *D. anceps* on temperature (2 °C/ 7°C) and culture treatments (mono/co-cultures). *n*=5. p-values were set to <0.05. TE = temperature, CU = culture treatment, ns = not significant. Significant values in italics.

Species	Parameter	Source of variation	Photosynthetic efficiency		
			df	F-value	p-value
D. menziesii	$rETR_{max}$	TE	1	0.1479	ns
		CU	1	0.0394	ns
		TE x CU	1	0.4863	ns
	α	TE	1	1.186	ns
		CU	1	3.235	ns
		TE x CU	1	6.505	*0.0214*
	Ek	TE	1	0.003	ns
		CU	1	0.4718	ns
		TE x CU	1	0.0226	ns
D. anceps	$rETR_{max}$	TE	1	2.0579	ns
		CU	1	0.5028	ns
		TE x CU	1	2.0178	ns
	α	TE	1	4.482	ns
		CU	1	0.022	ns
		TE x CU	1	1.311	ns
	Ek	TE	1	0.4051	ns
		CU	1	0.6997	ns
		TE x CU	1	1.1055	ns

Effets de la compétition interspécifique et du réchauffement global sur des espèces de Desmarestia endémiques de l'Antarctique

Résumé La Péninsule Antarctique Occidentale est une des régions avec le plus haut taux de réchauffement de la Planète dû aux changements climatiques, avec pour conséquence une diminution de la banquise et une augmentation de la sédimentation dans la colonne d'eau causée par la fonte des glaciers. Ces variations de lumière et température peuvent altérer la physiologie d'importants constructeurs d'écosystèmes tels que *Desmarestia menziesii* et *D. anceps*, influençant potentiellement leurs interactions. Cette étude a investigué les effets de différentes températures (2 contre 7 °C) et intensités lumineuses (10 contre 100 µmol m^{-2} s^{-1}) sur la réponse photosynthétique, la croissance et la compétition interspécifique de ces macroalgues antarctiques. *D. menziesii* et *D. anceps* de terrain ont montré un bas taux de croissance, cachant l'influence de température et lumière. Cependant, des températures élevées (7 °C) ont causé une diminution de l'efficience photosynthétique dans les deux espèces sous basses intensités lumineuses et encore plus prononcée sous haute intensité lumineuse, tandis que la combinaison 2°C et basse lumière n'a pas affecté leur photosynthèse. Aucun effet de compétition ou d'interaction entre compétition et température et/ou lumière n'a été détecté. La performance photosynthétique ($rETR_{max}$, α and E_k) et la concentration de Chlorophyll *a* en *D. anceps* ont été plus fréquemment affectées par la lumière élevée, révélant un comportement plus adapté à l'obscurité. Afin de comprendre quels facteurs contrôlent la zonation et la croissance de ces espèces clés de l'Antarctique sous un scénario de changement global, d'autres expériences multifactorielles incluant différentes étages de vie et processus reproductifs sont nécessaires.

Mots-clés : *Desmarestia anceps*, *Demarestia menziesii*, changement global, maximum quantum yield, macroalgues

Effects of interspecific competition and global warming on endemic Antarctic Desmarestia species

Abstract The Western Antarctic Peninsula is experiencing one of the fastest warming worldwide due to climate change showing decreased sea-ice cover and increased sedimentation in the water column due to glacial melt. Irradiance and temperature variations in the water column may alter the physiology of important ecosystem builders like the brown algae *Desmarestia menziesii* and *D. anceps* which form dense underwater forests in the upper to mid subtidal area, possibly influencing species interactions. This study examined the effects of different seawater temperatures (2 vs. 7 °C) and irradiance intensities (10 vs. 100 µmol m^{-2} s^{-1}) on the photosynthetic response, growth and interspecific competition of these cold-adapted Antarctic algae. Field *D. menziesii* and *D. anceps* showed very low growth rates, possibly reflecting a dormancy state which masked the influence of temperature and irradiance. However, increased temperature (7 °C) induced a decrease of optimum quantum yield of photosynthesis in both species under low but even more pronounced under high irradiance, whereas 2 °C combined with low irradiance did not affect their photosynthesis over two weeks. Neither interspecific competition nor interactions between competition and temperature and/or irradiance were detected. The photosynthetic performance ($rETR_{max}$, α and E_k) and Chlorophyll *a* concentration of *D. anceps* were more often affected by irradiance increases than of *D. menziesii*, reflecting an enhanced shade-adapted behavior. In order to understand which factors control the zonation and growth of these key Antarctic species under global change scenarios, further multifactorial experiments are of great importance, including different algal life stages and reproductive processes.

Keywords: *Desmarestia anceps*, *Demarestia menziesii*, global change, maximum quantum yield, seaweeds