Daily and seasonal changes of photobiological responses in floating bull kelp *Durvillaea antarctica* (Chamisso) Hariot (Fucales: Phaeophyceae)

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ABSTRACT: Floating seaweeds are important dispersal vehicles, especially for organisms with limited movement capacities and for the seaweeds themselves. The persistence of floating seaweeds is determined by the balance between their acclimation potential and the environmental pressures at the sea surface. Solar radiation is the most important inducer of physiological stress, varying in intensity throughout the day and the year. Therefore photoinhibition and subsequent recovery can change depending on the daily radiation dose and season. The bull kelp *Durvillaea antarctica* is one of the most common floating seaweeds in the southern oceans, including New Zealand, Chile, and most subantarctic islands. Herein, daily cycles of maximum quantum yield (F_v/F_m), photoinhibition and recovery levels were examined in microcosm experiments with floating *D. antarctica* throughout the year, focusing on the blade side exposed to solar radiation (sunny vs shadow side). Also, the effect of simulated wave action (blade turnover) and ultraviolet radiation (UVR) on photoinhibition and recovery of F_v/F_m was evaluated. Significant differences in maximum quantum yield were observed between blade sides, with lowest values on the sun-exposed side, especially during noontime and spring/summer months. Phlorotannins and pigments were measured during seasons with the most intense solar radiation (late spring, early summer), when F_v/F_m values were lowest. Phlorotannin, but not pigment concentrations, differed between sunny (lower concentration) and shadow blade sides (higher concentration) and throughout the daily cycle. Both blade sides had similar photoinhibition and recovery levels when blades were constantly turned over. Absence of UVR favoured the recovery capacity of F_v/F_m in both blade sides, suggesting that the photorecovery potential of floating kelps depends on the environmental conditions that kelp rafts face at the sea surface (e.g. cloudy vs sunny days, intense seawater movement and splashing vs calm sea conditions). The results confirm that photobiological stress is more severe during summer and on continuously sun-exposed blade sides, thereby damaging the blades and suppressing the floating time of *D. antarctica*.

KEY WORDS: *Durvillaea antarctica*, Floating kelps, *in vivo* fluorescence, Photoinhibition, Recovery, Solar radiation

INTRODUCTION

Changes in solar radiation, including both photosynthetically active radiation (PAR) and ultraviolet radiation (UVR), can occur over short (daily) and long (seasonal) scales, affecting biochemical and physiological processes in higher plants as well as in seaweeds (Hurd *et al.* 2014). Temperature and solar radiation are generally correlated in surface seawaters, providing a synergistic effect on algal physiology and growth (Lüning & tom Dieck 1989; Bruhn & Gerard 1996; Bearham *et al.* 2013).

Dynamic photoinhibition of photosynthesis is considered an important defensive response. Photoinhibition limits the photosynthetic electron transport through photosystem II (PSII) and diverts excess excitation energy by thermal dissipation. This protects important cellular components such as D1 proteins in the photosynthetic apparatus and DNA (Powles 1984; Long *et al.* 1994). In marine habitats, daily and seasonal variations in irradiance (Häder & Figueroa 1997; Huovinen *et al.* 2006), light attenuation across vertical gradients (Hanelt *et al.* 1997; Gómez &

Huovinen 2011), sediment load (Roleda & Dethleff 2011) and irregular light fluctuations due to water turbulence (Wing & Patterson 1993) are factors that influence algal photosynthetic efficiency and photoinhibition levels. Continuous movements of seaweeds by wave action produce an irregular and short-term variability of light availability across the thallus surface (i.e. light vs shading pulses) that might also reduce radiation stress, thereby enhancing algal photosynthetic performance (Dromgoole 1987; Greene & Gerard 1990; Wing & Patterson 1993; Wing *et al.* 1993). Biochemical responses such as production of secondary metabolites (in brown seaweeds, mainly phenolic compounds such as phlorotannins) can serve as photoprotective and antioxidant mechanisms, thus minimizing the photodamage caused by solar radiation (Huovinen *et al.* 2006; Cruces *et al.* 2012; Abdala-Díaz *et al.* 2014).

The lifetime of most benthic seaweeds depends on their ability to remain attached to the substratum, but some environmental conditions (e.g. storms, herbivory) or aging provoke detachment and subsequent death. Nevertheless, some seaweeds feature morphological adaptations such as gas-filled structures and tissues that allow them to float at the sea surface for periods of weeks or months before disintegrating or stranding on shores (Hobday 2000; Hernández-Carmona *et al.* 2006; Graiff *et al.* 2013; López

et al. 2016). Quick physiological adjustment and continuous production of biomass are key adaptations that determine rafting time and dispersal potential under the challenging environmental conditions at the sea surface (Hernández-Carmona et al. 2006; Vandendriessche *et al.* 2007; Rothusler *et al.* 2011a, b, c; Graiff *et al.* 2013). High radiation and temperatures cause tissue disintegration and diminish photosynthetic capacities, thereby suppressing the floating time of buoyant seaweeds at temperate latitudes (Vandendriessche *et al.* 2007; Rothäusler *et al.* 2011a; Graiff *et al.* 2013).

Durvillaea antarctica (Chamisso) Hariot (Fucales, Phaeophyceae), the buoyant bull kelp, has an extensive geographic range in the Southern Hemisphere, including New Zealand, Chile, and most subantarctic islands (Hay 1994; Fraser *et al.* 2010). The blades of adult individuals of *D. antarctica* have a well-developed medullary tissue that resembles an air-filled honeycomb structure, which provides high positive buoyancy that permits it to float over long distances (Hay 1994; Fraser *et al.* 2010). This species is one of the most common floating seaweeds in the southern oceans (Smith 2002), including the fjord region of southern Chile (Hinojosa *et al.* 2010; Wichmann *et al.* 2012) and the continental coast of central Chile (Tala *et al.* 2013; López *et al.* 2016).

The thick leathery blades of *Durvillaea antarctica* can have a thickness of 2 to 3 cm due to the medullar tissue development that produced a thallus absorptance > 90 % between 300 and 700 nm (Gómez & Huovinen 2011). This morphological and bio-optical condition isolates the sides of photosynthetic blades from each other with a minimum light penetration through the honeycomb. Thereby the two blade sides are exposed to different light conditions in the natural habitat. The high buoyancy and size of *D. antarctica* lead to a particular floating pattern wherein one blade side of the detached individual is continuously exposed to sun (i.e. direct radiation) and air with low potential for overturn. In contrast, the other side of the blade is shaded and below the sea surface, receiving indirect solar radiation by reflection and scattering through seawater. Unilateral solar stress might produce physiological damage, tissue degradation and biomass loss, mainly on one blade side, whereas the other side of the blade is less stressed and physiologically competent. Some metabolic connections through the sides of the blade can occur by sieve elements as described for Fucales (Raven 2003), whereby the metabolic production on the shadow side might provide energy required for photoprotective responses on the sunny side of the blade. Deleterious effects are expected to occur especially during the summer months, when e.g. at 39°S the intensity of solar radiation can be up to 37 times higher than in winter (Huovinen *et al.* 2006). Light fluctuation due to wave movements, splashing and turnover of floating *D. antarctica* would reduce the risk of photodamage. In this situation, both sides of the blade are regularly hydrated, shaded and protected from the direct impact of solar radiation, enhancing the recovery capacity of *D. antarctica* blades in a similar way as occurs in their wave-exposed benthic habitat by the whiplash movement of the blades (Wing & Patterson 1993; Stevens *et al.* 2002). Thus, in areas or during periods with strong winds and waves, there should be minor photobiological damage due to the continuous movement and splash of the floating kelp blade at the sea surface.

In this study we examined the hypotheses that (1) photobiological damage of floating kelp blades is higher during the summer months than during the rest of the year (by a combined effect of high-dose radiation and temperature), and (2a) frequent turnover of blades and (2b) absence of UVR reduce photodamage by enhancing the recovery potential. To test these hypotheses we determined the daily and seasonal variation in the photosynthetic performance (maximum quantum yield F_v/F_m, photoinhibition and recovery of photosynthetic activity) separately on the two opposite blade sides of *Durvillaea antarctica*. During the seasons with the strongest solar radiation (late spring/early summer), the daily dynamics of pigment and phlorotannin levels were additionally determined in both blade sides.

MATERIAL AND METHODS

Specimens of *Durvillaea antarctica* were collected during low tide in the rocky intertidal zone of Puerto Oscuro, Chile (31°25′S, 71°38′W), at the northern distribution limit of this kelp in the southeastern Pacific (Collantes *et al.* 2002; Fraser *et al.* 2010). Molecular studies had shown that the populations from central Chile (30–44°S) are genetically different from the populations of southern Chile (49–56°S) (Fraser *et al.* 2010), and the current study focuses on the clade from central Chile.

Every 2 mo between November 2010 and January 2012, 10 kelp individuals were collected with an average weight of 2.68 ± 1.97 kg ($\bar{X} \pm s$) and a length of 1–3 m. The thickness of the medulla in *Durvillaea antarctica* is not homogenous across the blade and depends on different factors such as wave exposure, age and blade growth (Hay 1994). To minimize the potential effects of variable blade thickness on the photoinhibition/recovery responses, similar-sized individuals with well-developed medullar tissues were selected. Collected kelps were then maintained overnight in a 2000-litre tank covered with a black plastic mesh and with a constant flow of running seawater until used in the experiments.

During each experiment the daily cycle of PAR (400–700 nm), UV-A (340–400 nm) and UV-B (290–340 nm) radiation was measured using a Li-190SA quantum sensor (LI-COR Bioscience, Lincoln, Nebraska, USA), UV3pA and UV3pB sensors (Delta-T Devices Ltd., Cambridge, UK), respectively, connected with a LI-1400 data logger (LI-COR Bioscience). The sensors were close to the experimental surface and radiation was recorded between 7:00 AM and 7:00 PM at 15-min intervals. Similar systems were used in our previous studies (Graiff *et al.* 2013; Tala *et al.* 2013). The instantaneous radiation levels were used to calculate the daily dose (kJ m^{-2}) for each month for the duration of each experiment. The temperature in each experimental container was recorded every 2 h with a handheld thermometer (HI93510, HANNA Instruments, Cluj, Romania).

Experiments evaluated the daily variation in maximum quantum yield of floating thallus pieces of *Durvillaea antarctica* under natural solar radiation at temperate

latitudes (30°S) in outdoor microcosms. In the experiments the samples were placed in 10 transparent plastic containers (2.2l –20 cm × 14 cm × 8 cm deep). Microfiltered (1 μm) seawater was pumped from La Herradura Bay–Coquimbo (29°58′S, 71°21′W), and seawater was continually flowing through each container at approximately 0.9 l min^{-1}. The attenuation of light inside the plastic containers was ∼20%.

In the morning [7:00 AM, Greenwich Mean Time–3:00 AM in austral summer], small pieces of kelp blades were cut for the experiments (approximately 15 cm long and 10 cm wide). Previous studies had shown that small thallus pieces of photosynthetically active tissues are suitable to determine physiological responses, especially in large marine seaweeds (e.g. Hanelt *et al.* 1997; Bischof *et al.* 1998; Rothäusler *et al.* 2011a; Cruces *et al.* 2012; Gao *et al.* 2017). Each blade piece was carefully cleaned with a paper towel to remove any epibionts from its surface. The two blade sides were randomly assigned as 'sunny' and 'shadow', with the sunny side always referring to the upper side exposed to direct solar radiation, and the shadow side referring to the opposite, lower side, which only received indirect radiation from the surrounding water and container walls.

For each experimental month (seasonal variation), three daily cycles of maximum quantum yield were done for consecutive days under different experimental conditions. In the first daily cycle, henceforth referred to as 'static cycle', the blade pieces were maintained in a static condition ($n =$ 10), with always the same side of the blade exposed to direct and the other to indirect (reflected and scattered) solar radiation throughout the entire experiment. The static daily cycle of the maximum quantum yield (F_v/F_m) was measured every hour from 8:00 AM until 8:00 PM, and at 8:00 AM of the subsequent day to measure the recovery capacity.

In the second daily cycle, referred to as 'turnover cycle', the effect of wave agitation and occasional tumbling on the photosynthetic respones of the kelp pieces was evaluated. Blade pieces that were regularly turned over were compared with those that were maintained in static conditions (identical to the static cycle). After 1 h of exposure to solar radition of each blade piece ($n = 10$) in initial static conditions (between 8:00 AM and 9:00 AM), measurements of F_v/F_m were taken as initial value for the sunny and shadow sides. Thereafter, in five random containers, blade pieces were turned over every 10 min, such that sunny and shadow sides were exposed alternately to direct and indirect solar radiation, whereas the other five blade pieces were maintained in static conditions (without turnover). To simulate strong wave conditions in the open ocean, turnover of kelp tissue pieces was done every 10 min, a frequency that is considered conservative as real turnover time in natural conditions is most likely higher. Although the sunny and shadow sides are continuously changing in the turnover treatment, the identification of the initial blade position was registered to compare between the sides with the static treatment. The maximum quantum yield (F_v/F_m) of the differently treated kelps was measured every 2 h between 09:00 AM and 7:00 PM, at 8:00 PM of the same day and then at 8:00 AM of the following day to evaluate recovery. On the basis of the daily variation of F_v/F_m during the static cycle (first daily cycle), a sampling time of every 2 h was considered appropriate to evaluate the photobiological responses in turnover conditions.

To evaluate the effect of UVR) on recovery of chlorophyll fluorescense (F_v/F_m), a third daily cycle, referred to as 'UVR cycle', was conducted in full solar radiation (PAR + UVR) and without UVR (PAR) conditions. After exposing the kelp pieces for 1 h to full natural radiation (between 9:00 AM and 10:00 AM), initial values of F_v/F_m were measured at 10:00 AM on both blade sides separately. Afterward, five randomly selected containers with blade pieces were kept under PAR conditions (Ultraphan 395-nm folder, 0.12 mm, Digefra, Munich, Germany), and the other five containers were maintained under PAR + UVR conditions (Ultraphan, 295-nm folder, 0.3 mm, Digefra). The maximum quantum yield was measured again at 2:00 PM, and then the containers were covered with a black mesh to induce recovery of photosynthesis by reducing the incoming solar radiation (see also Rothäusler *et al.* 2011a). The maximum quantum yield in each condition and on both blade sides was measured at 4:00 PM, 6:00 PM and 8:00 PM, respectively, and at 8:00 AM the next day. The blades were maintained static during the entire experimental time, without turning them over. The PAR and UVR attenuation beneath the black mesh was > 90% (portable quantometer MQ-200 and MU-200 respectively, Apogee Instruments, Logan, Utah, USA).

For the evaluation of the daily maximum quantum yield of PSII, two samples were taken from each blade piece with a cork borer of 13-mm diameter, and then the blade piece was put back in the experimental container in the original position. A transverse cut through the medullar tissue was done to separate the tissue section corresponding to the sunny and the shadow sides. Sample discs were maintained for 20 min in darkness before the measurements. The maximum quantum yield of chlorophyll *a* (Chl *a*) fluorescence (PSII) was measured *in vivo* with a portable fluorometer (PAM 2500 Waltz, Effeltrich, Germany). Measurements of F_v/F_m were done randomly and each sample disc was represented by an average from two measures.

For each daily cycle, the effect of the different experimental conditions on photoinhibition ($Ph_{Fv/Fm}$) and recovery ($Rec_{Fv/Fm}$) were expressed as percent values in relation to the initial value $I_{Fv/Fm}$ of maximum quantum yield. Photoinhibition was calculated after Bruhn & Gerard (1996) using the equation:

$$Ph_{Fv/Fm} = 100 - \left[100 \times (L_{Fv/Fm}/I_{Fv/Fm})\right]$$

where $L_{Fv/Fm}$ is the lowest value of maximum quantum yield found at noon. Recovery of PSII ($Rec_{Fv/Fm}$) from photoinhibition was calculated with F_v/F_m values at the next day with the following equation:

$$Rec_{Fv/Fm} = 100 \times (F_{Fv/Fm}/I_{Fv/Fm})$$

where $F_{Fv/Fm}$ is the final value of maximum quantum yield at the end of recovery (8:00 AM the next day). Full recovery of PSII should be reached when final values are similar to initial levels as suggested by Roleda *et al.* (2006), and $Rec_{Fv/Fm}$ approaches a value of 100.

In November 2011 and January 2012, tissue samples for soluble phlorotannin and pigment analyses were taken during the static cycle in a parallel set of experimental containers that were run specifically for this purpose. Ten independent blade pieces were used and the initial sampling was done at 8:00 AM, and then at 2:00 PM and 8:00 PM of the same day, and at 8:00 AM on the following day. Sunny and shadow samples were separated with a transverse cut in the medullar zone, frozen in liquid nitrogen, and later stored at −80°C. The analysis methods are the same used in previous studies with floating kelps (Rothäusler *et al.* 2011a; Graiff *et al.* 2013; Tala *et al.* 2013).

The analysis of soluble phlorotannins was done with the Folin–Ciocalteu method as described in Gómez & Huovinen (2010) for ground dry samples. Three successive extractions were done for each sample [∼15 mg dry weight (DW)] with 70% acetone for 12 h at 4°C. The absorbance was read at 730 nm in a multiscan spectrophotometer (Multiskan Spectrum 1500, Thermo Scientific, Vantaa, Finland) in a mixture of 100 μl of the extract, 100 μl of distilled water, 100 μl of Folin–Ciocalteu 1 N and 200 μl of 20% p/v $NaCO_3$. The content of phlorotannins was expressed as mg g^{-1} DW and purified phloroglucinol (Sigma Aldrich, San Luis, Missouri, USA) was used as a standard.

For pigment extractions (Chl *a*, Chl *c* and total carotenoids) 15 mg of biomass [wet weight (WW)] was used for each sample, which was then incubated in the dark for 24 h at 4°C with 2 ml of N,N-dimethylformamide. Absorbances were quantified in a spectrophotometer (Spectro UV-2650, Labomed, Inc., Los Angeles, USA). Pigment content was calculated using the equations of Inskeep & Bloom (1985) for Chl *a* and those of Henley & Dunton (1995) for Chl *c* and total carotenoids. The values were expressed in mg g^{-1} WW.

The daily variation in F_v/F_m was analyzed for the static cycle experiment with a repeated-measures analysis of variance (ANOVA) for one between factor and two within factors. Month was considered as the between independent factor, because new kelps were collected bimonthly for each experiment (see above). Time of the day when seaweeds were measured was considered as a within factor as during the day the samples were taken from the same replicate. The two kelp sides were considered as the second within factor, because measurements of the sunny and shadow sides were taken from the same replicate. Ten replicates were considered for each combination of factors, leading to a balanced design.

In the three daily cycle experiments, the F_v/F_m recovery for the day after the photoinhibition was analysed using a linear mixed-effects model with R (R Core Team 2013) and lme4 (Bates *et al.* 2014). Month was considered a fixed effect because new kelp samples were collected bimonthly for the experiments (see above). Photoinhibition was also considered in the models because its effect was highly and inversely correlated with the recovery obtained in the experiments. In the first experiment (static cycle) month was considered as a main treatment; in the second experiment (turnover cycle) the effect of rotation (static or turnover) and in the third experiment (UVR cycle) the effect of solar irradiation (PAR or PAR + UVR) were included in the respective analysis. The side of the kelp (sunny or shadow) was considered as a random effect in the three analyses because of dependency of

the two measures made on the kelp samples. Both the intercepts and the slopes for the effect of recovery were left to vary randomly across model estimations. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. *P*-values for the three experiments were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question.

In the experiment to evaluate phlorotannin and pigment changes during the static daily cycle in two seasons (November 2011–late spring, and January 2012–early summer), a total of five response variables was obtained from each side (sunny and shadow) of the same replicate. Considering the dependence (sunny and shadow sides sampled at different times of the day from the same replicate), a three-way nested model of a multivariate ANOVA (MANOVA) was considered most appropriate to determine significant effects (Quinn & Keough 2002). The main factor was month, the first nested factor was time of the day (four levels) and the second nested factor was side of the kelp (two levels). The analysis was done using SYSTAT v.13 (SYSTAT Software, Inc, Chicago, Illinois, USA).

RESULTS

Environmental conditions

During the course of experimentation, the environmental variables of radiation and temperature showed the expected seasonal variation. The daily radiation dose was lowest during the austral autumn/winter (March–September) and highest in summer (Fig. 1). The seasonal pattern was more notable for PAR and UV-A, with spring/summer values being almost twice as high as the fall/winter values (Fig. 1). Seawater temperatures also showed seasonal variations, with temperatures ranging from 12.8°C to 14.1°C in winter, and from 16.7°C to 19.3°C in summer (Fig. 1). The lowest daily temperatures were generally in the morning (8:00 AM) and the highest in the afternoon (3:00–5:00 PM).

Daily cycles of photobiological performance

The maximum quantum yield (F_v/F_m) during the static cycle showed a clear daily fluctuation with highest values in the morning and late afternoon, and lowest values in the early afternoon (Fig. 2). This pattern was observed during all months and for both blade sides in accordance to daytime PAR variations (Fig. 2). During the midday peak of solar radiation (between 12:00 and 4:00 PM), F_v/F_m was minimal, especially on the sun-exposed blade side. In September 2011 (early spring), when the lowest PAR levels occurred, the daily decrease in F_v/F_m was relatively minor compared with the other months (Fig. 2). The maximum quantum yields were especially low in November 2011 and January 2012, corresponding to late austral spring and early summer PAR, respectively (Fig. 2). Overall, F_v/F_m differed significantly for each tested factor (month, time, blade side), as well as for their interactions (Table 1).

The turnover and UVR cycles showed similar patterns in the daily variation of F_v/F_m (Figs S1, S2). Photosynthetic
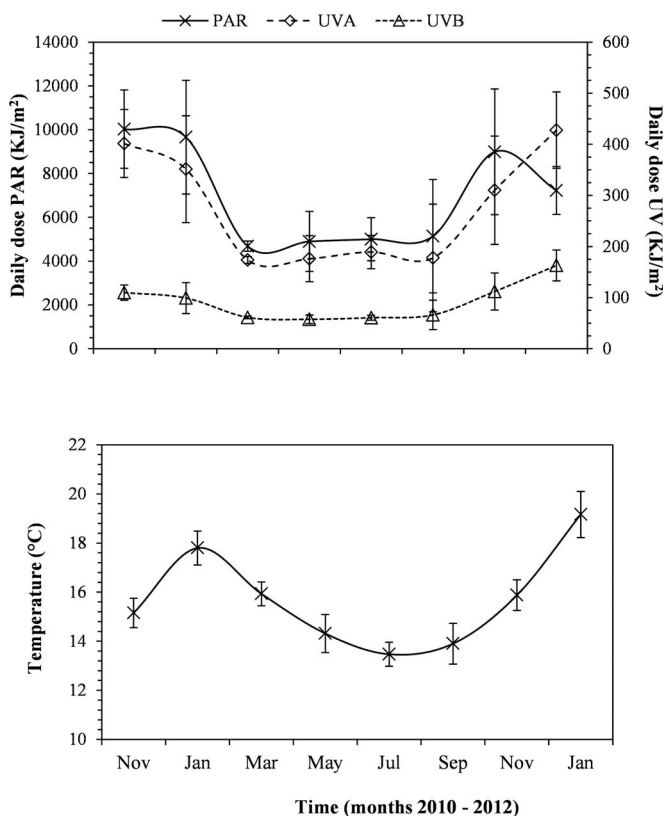
Fig. 1. Seasonal variation in daily dose of solar radiation for PAR and UVR (upper panel) and seawater temperature (lower panel) measured in experimental containers during the three cycle experiments. Each point represents the mean ± standard deviation between the three experimental days and for every month.

efficiency was lowest on the sunny side and during spring/ summer; this effect was more notable in the static than in the turnover treatment (Fig. S1). Moreover, in the turnover treatment, there were no clear differences in F_v/F_m between blade sides. Similar values were detected between radiation treatments (PAR vs PAR + UVR), sides and months (Fig. S2). As the blades in both experimental treatments were shaded after 2:00 PM, they started to recover during the afternoon,

Table 2. Summary of the three-way nested MANOVA test for the physiological response (F_v/F_m, phlorotannins) of *Durvillaea antarctica*. Main factor was month (November 2011 and January 2012), first nested factor was time of the day (8:00 AM, 2:00 PM, 8:00 PM and 8:00 AM recovery) and second nested factor was blade side of the kelp (sunny and shadow). Results of the univariate test are given for the response variables in which significant effects of the factors were identified. See text for details (full MANOVA is given in the online supplements, Table S1).

	Month	Time (Month)	Side [time (Month)]
Multivariate Test Statistics			
Wilks's lambda	0.4997	0.1149	0.1423
F-ratio	12.0133	5.7886	3.7285
df	5, 60	30, 242	40, 264
P	< 0.001	< 0.001	< 0.001
Univariate *F*-tests			
Response variables, *P*			
F_v/F_m	< 0.001	< 0.001	< 0.001
Phlorotannins	< 0.001	0.0176	0.0426

reaching similar or higher than initial F_v/F_m values by the end of the day and maintaining these until the next day (Fig. S2).

Variations in the concentrations of metabolites (phlorotannins and pigments) were observed in November 2011 and January 2012 on both blade sides during the daily cycle. The three-way nested MANOVA showed that F_v/F_m and phlorotannin concentrations differed significantly between months ($P < 0.001$), time of the day ($P < 0.05$) and for blade sides ($P < 0.05$) (Table 2; Table S1). In general, higher phlorotannin concentrations were found in January 2011 on the shadow side but the daily pattern depended on the month (Fig. 3). In November 2011, phlorotannin concentrations appeared not to change during the day, whereas in January 2012 a decrease in the concentration was observed toward the afternoon on both blade sides (Fig. 3).

Photoinhibition and recovery of F_v/F_m

The capacity of the floating kelps to recover their photosynthetic performance after photoinhibition partially depended on experimental conditions and photoinhibition levels (Figs 4, 5). In addition, photoinhibition was highly dependent on solar radiation, which varied between months according to seasonal

Table 1. Results of repeated-measures ANOVA for the static daily cycle experiment to study the photosynthetic performance (F_v/F_m) of *Durvillaea antarctica*. Data were evaluated with a repeated-measures ANOVA between (months) and within subjects. The within subjects were time of the day and blade side (sunny and shadow) of each replicate.

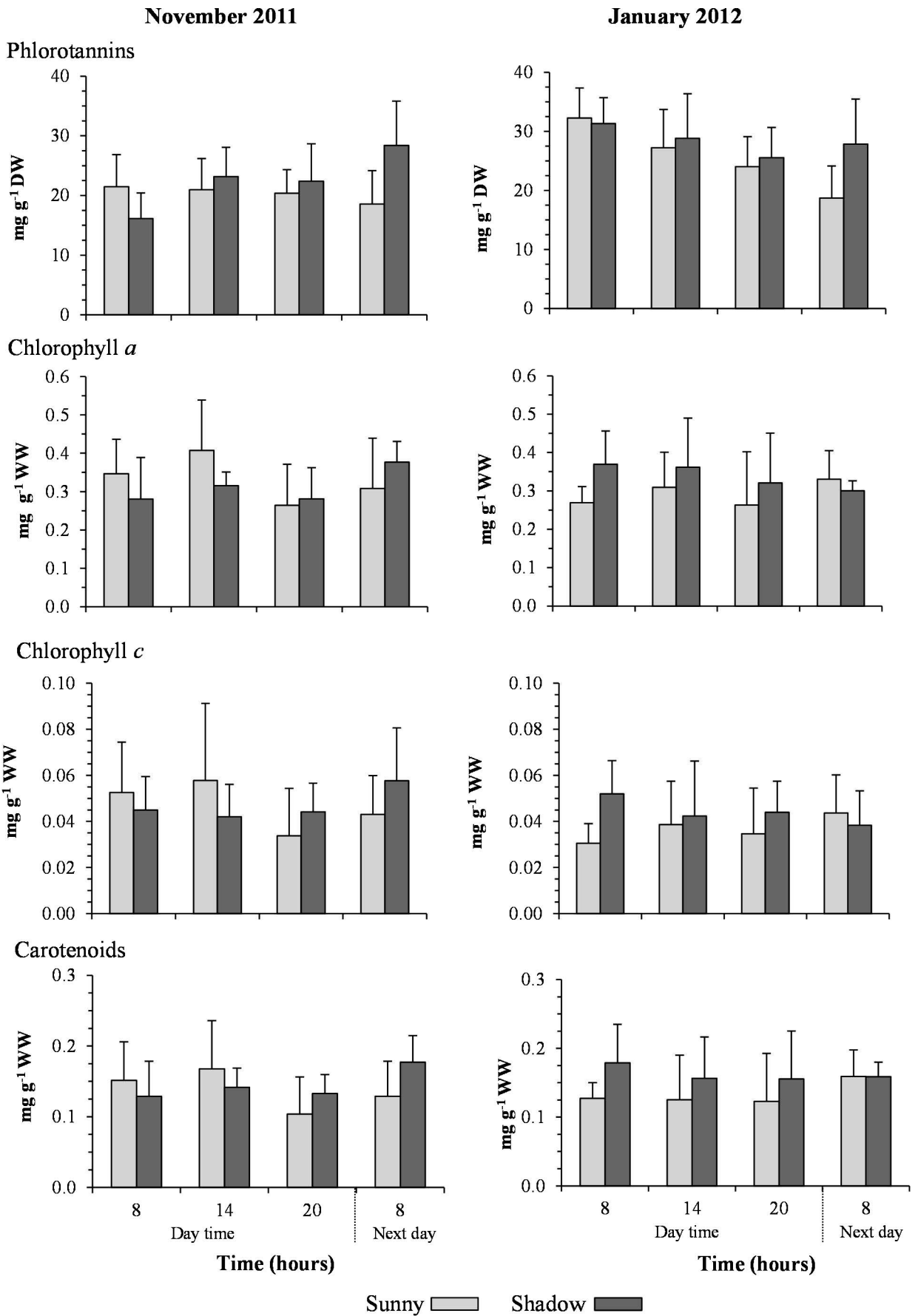|	Sum of squares	df	Mean square	*F*-ratio	*P*-value
Between subjects					
Months	18.6945	5	3.7389	155.9097	< 0.0001
Error	1.2950	54	0.0240		
Within subjects					
Time	20.0057	13	1.5389	689.6987	< 0.0001
Time × months	4.3377	65	0.0667	29.9085	< 0.0001
Error	1.5664	702	0.0022		
Side	9.0985	1	9.0985	1,037.9326	< 0.0001
Side × months	0.5568	5	0.1114	12.7035	< 0.0001
Error	0.4734	54	0.0088		
Time × side	1.0700	13	0.0823	38.7405	< 0.0001
Time × side × months	1.1923	65	0.0183	8.6337	< 0.0001
Error	1.4914	702	0.0021		
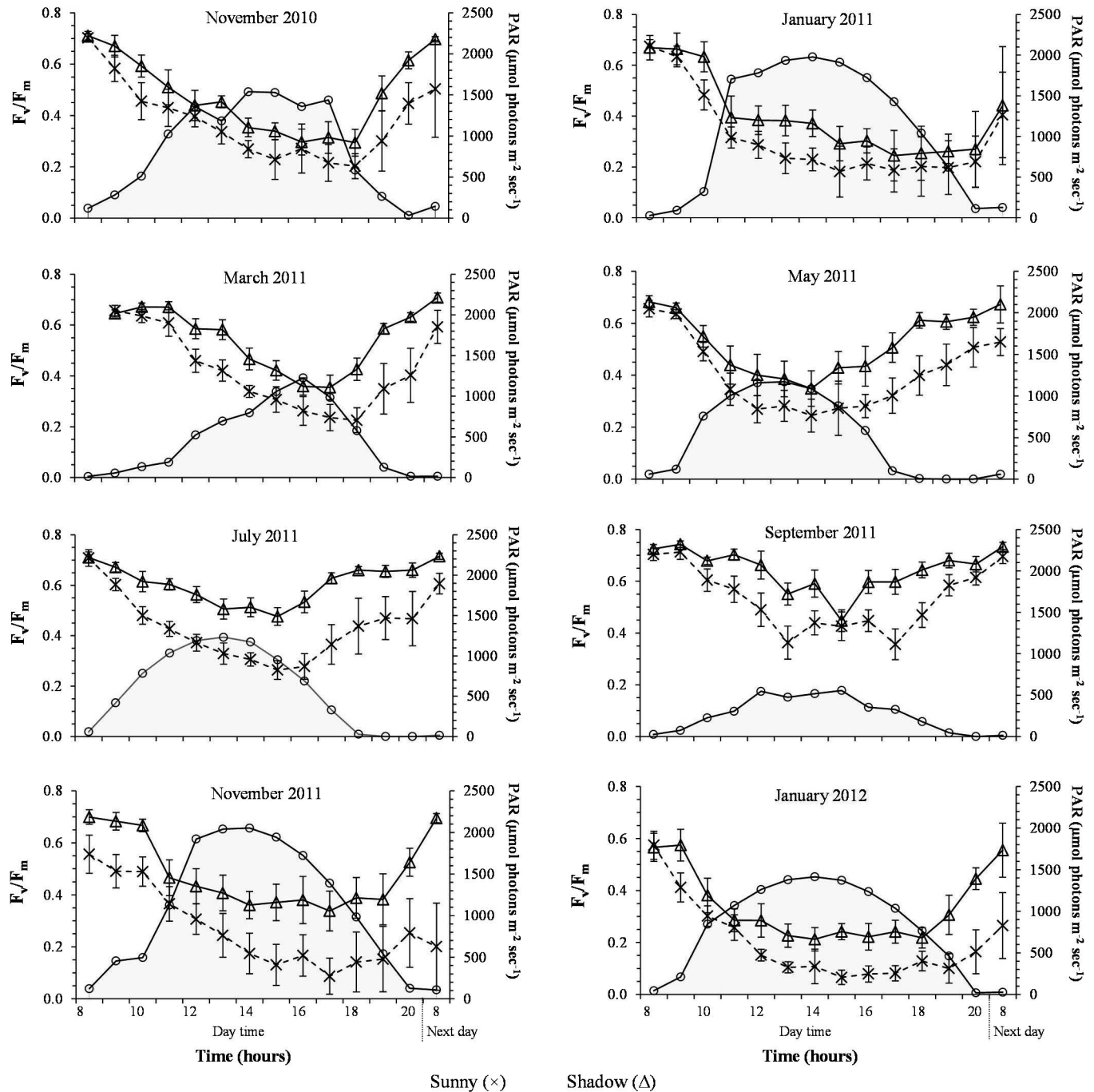
Fig. 2. Seasonal variation in the static daily cycle of maximum quantum yield (F_v/F_m) of *Durvillaea antarctica* blades in experimental tanks. Diurnal pattern of irradiance (PAR, µmol photons m^{-2} s^{-1}) is shown as grey shading. Each point represents the mean ± standard deviation of 10 replicates for sunny (×) and shadow (Δ) sides.

changes. The linear mixed models revealed no significant effects of month on the recovery of the F_v/F_m values during the static cycle ($P = 0.0863$; Table 3). However, the interaction between month and photoinhibition in the static cycle was

highly significant ($P = 0.0006$) for recovery capacity, reflecting the negative effect of higher solar radiation during summer. In the static cycle, no significant effect ($P > 0.05$) of blade side was detected on recovery capacity. Both blade sides showed

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Fig. 3. Phlorotannin and pigment concentrations in *Durvillaea antarctica* during late spring and early summer (November 2011 and January 2012) in the static daily cycle. Light grey columns represent the mean (± standard deviation) for the sunny side and dark grey columns represent the shadow side of the blade.
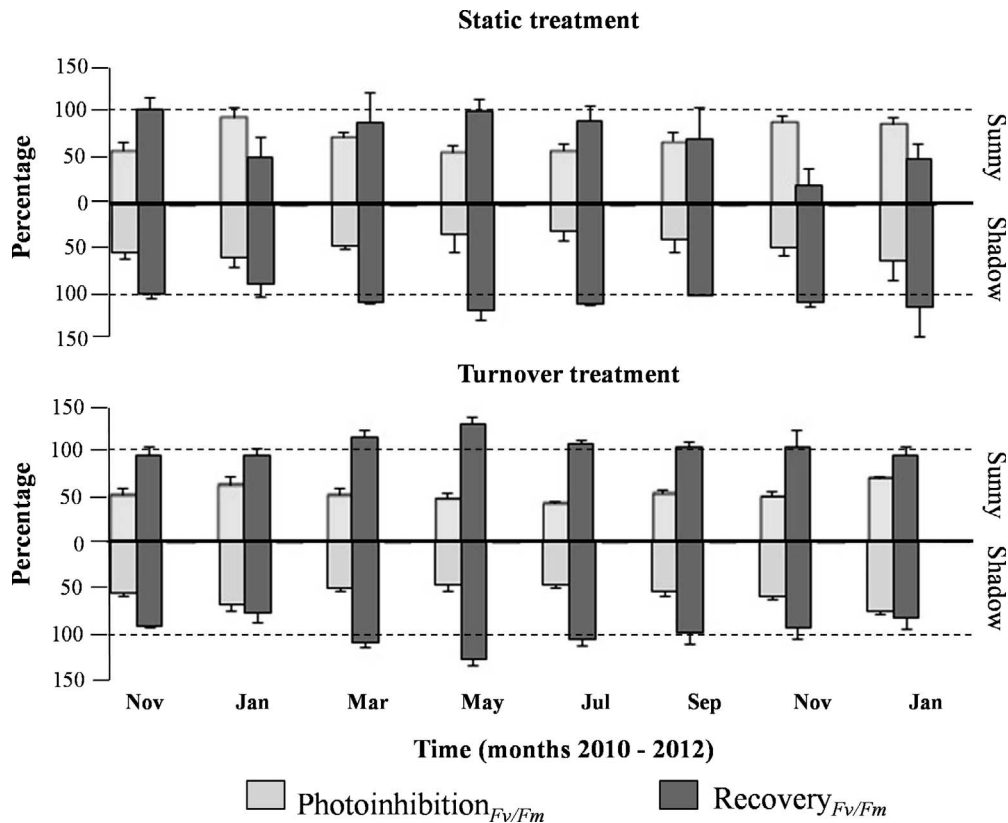
November 2011   **January 2012**

Phlorotannins

Chlorophyll *a*

Chlorophyll *c*

Carotenoids

Time (hours)

Sunny ☐   Shadow ■

Static treatment

Turnover treatment

Time (months 2010 - 2012)

☐ Photoinhibition$_{Fv/Fm}$ ■ Recovery$_{Fv/Fm}$

Fig. 4. Seasonal variation of photoinhibition and recovery (%) in *Durvillaea antarctica* in relation to initial values of F_v/F_m during turnover daily cycle. In both cases initial values were set at 100% (dashed line, see details in Material and Methods). Light grey columns represent the photoinhibition and dark grey columns represent the recovery. Each point represents the mean ± standard deviation of five replicates.

recovery in F_v/F_m values after the night, but recovery tended to be less efficient on the sunny side during summer.

During the turnover cycle, higher photoinhibition and lower recovery capacities were observed on the sunny blade side, especially in the static treatment (Fig. 4). In this treatment, photoinhibition of the sunny blade side occurred in all months and was particularly evident during summer, where lower F_v/F_m persisted until the next day (Fig. 4). Additionally, an increase in photoinhibition was also detected on the shadow side during summer (January 2011 and January 2012: 58% and 62%, respectively), but the recovery of F_v/F_m was almost complete, reaching > 87% in both cases (Fig. 4,

Fig. S1). In the turnover treatment, there were no clear differences in photoinhibition and recovery capacities between blade sides. Recovery of the experimental kelps was significantly ($P = 0.0059$) affected by the experimental treatment (static vs turnover; Table 3). Recovery capacity decreased by ~6% ($s_{\bar{X}} = 2.100$, $P = 0.0059$) when experimental kelp pieces were maintained static compared with those that were continuously turned over. Furthermore, the recovery of the experimental kelp pieces was significantly affected by month ($P = 0.0264$) and also by the interaction with photoinhibition ($P < 0.0001$) (Table 3). Similar to the first static cycle, blade side did not significantly ($P > 0.05$) affect recovery, but in

Table 3. Linear mixed models for the effects of recovery (F_v/F_m) and photoinhibition of *Durvillaea antarctica* submitted to several effectors. The results for the three experiments are summarized. The random effects of blade side of the seaweed did not significantly ($P < 0.05$) affect recovery (see text for details).

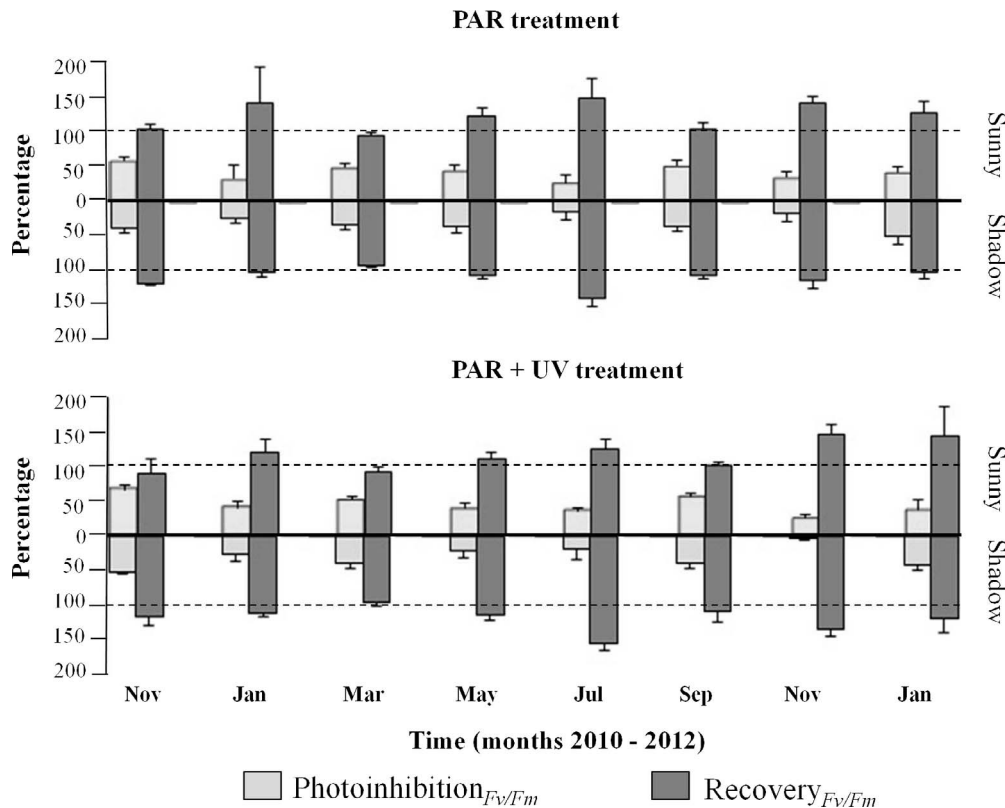| Effect	Numerator df	Denominator df	F-ratio	P-value
Static cycle				
Month	7	7	2.981	0.0863
Month × photoinhibition	8	131	3.722	0.0006
Turnover cycle				
Month	7	7	4.888	0.0264
Static/turnover	1	134	7.825	0.0059
Month × photoinhibition	8	134	5.753	0.0001
UVR cycle				
Month	7	7	3.285	0.0696
PAR/PAR + UVR	1	134	4.879	0.0288
Month × photoinhibition	8	134	5.181	0.0001

Fig. 5. Seasonal variation of photoinhibition and recovery (%) of *Durvillaea antarctica* in relation to initial values of F_v/F_m during the UVR daily cycle. In both case initial values were set at 100% (dashed line, see details in Material and Methods). Light grey columns represent the photoinhibition and dark grey columns represent the recovery. Each point represents the mean ± standard deviation of five replicates.

November 2011, January 2011 and January 2012 recovery of the sunny blade sides in the static treatment was very low (Fig. 4), probably as a result of the interactive effect between month and photoinhibition.

In the UVR cycle, solar radiation had a significant effect on the capacity of the kelp pieces to recover initial values of F_v/F_m ($P = 0.0288$). Experimental kelps that were exposed to PAR only (without UVR) had recovery that averaged 5% ($s_{\bar{X}} = 2.071$; $P = 0.0288$) higher than kelp pieces that were exposed to all components of solar irradiation (PAR + UVR) (Fig. 5). Recovery of experimental kelps maintained under the UVR treatment was not significantly affected by seasonality (month in our model) ($P = 0.0696$), but the interaction of month with photoinhibition was highly significant ($P = 0.0001$; Table 3). As in the other daily cycles, blade side did not affect recovery ($P > 0.05$; Table 3): sunny blade sides were able to recover in the same way as shadow sides (Fig. 5).

DISCUSSION

Daily acclimation in photosynthetic performance of *Durvillaea antarctica* depended on season, floating conditions and blade side. Increase of photoinhibition and a decrease in recovery capacity was more notable at high irradiance conditions, i.e. during summer and on the sunny blade side. Nevertheless, some floating conditions (e.g. continuous blade turnover, reduced daily dose of radiation) helped to mitigate the negative effects of solar radiation and temperature on floating kelps. Thus, intrinsic (photoacclimation potential, defense metabolites) and extrinsic factors (wave agitation of kelps, daily dose of radiation) determine the floating persistence of this bull kelp.

Daily cycle of photosynthesis and metabolites

Daily photosynthesis cycles for many plants, seagrasses and seaweeds generally show a decreasing activity around noon (Long *et al*. 1994; Silva & Santos 2003; Cabello-Pasini *et al*. 2000; Kokubu *et al*. 2015; Terada *et al*. 2016). We observed relatively strong diurnal changes in photosynthetic performance of *Durvillaea antarctica* relative to daily light cycles with maximum quantum yield, with low F_v/F_m during early afternoon. This was consistent throughout the year for blade sides and experimental conditions. The decrease in the quantum yield of PSII is understood as a dynamic defensive mechanism in response to high irradiance. This avoids the photo-oxidative destruction of the photosynthetic apparatus and probably dissipates excess energy as heat (Häder & Figueroa 1997; Gómez *et al*. 2004; Gao & Xu 2010). Daily variations in maximum quantum yield were described for seaweeds *in situ* (Hanelt *et al*. 1993; Edwards & Kim 2010; Kokubu *et al*. 2015), as well as in outdoor (Cabello-Pasini *et al*. 2000; Cruces *et al*. 2013) and indoor culture tanks (Gómez *et al*. 2004; Abdala-Díaz *et al*. 2006; Terada *et al*. 2016). Accordingly, experimental conditions can help to understand the photosynthetic performance of *D. antarctica* during the first 24 h of floating.

Phlorotannins, which are important secondary metabolites of brown seaweeds, have multiple functions due to their high antioxidant and photoprotective capacity (Swanson & Druehl 2002; Gómez & Huovinen 2010; Steinhoff *et al.* 2011). The adjustment of phlorotannin concentrations as a defensive response is a complex interaction between processes of exudation, photodegradation and synthesis. All of these can fluctuate on daily, seasonal and geographic scales (Van Alstyne *et al.* 1999; Connan *et al.* 2004, 2007; Abdala-Díaz *et al.* 2006, 2014). Herein, phlorotannins showed dynamic intraday changes, suggesting that variations are induced by photosynthetic stress due to an increase in solar radiation, as has also been reported for other brown seaweeds (e.g. Abdala-Díaz *et al.* 2006; Cruces *et al.* 2012, 2013). Lower phlorotannin values on the sunny blade side of *Durvillaea antarctica* could be caused by phenolic exudates and photodegradation. Laboratory experiments showed that phenolic compounds can photo-oxidize under visible light conditions ($\lambda > 420$ nm) (Kim & Choi 2005). The differences observed between spring and summer could be due to seasonal photoadaptive processes of acclimation in the field (Cabello-Pasini *et al.* 2000), as had also been observed in other seaweeds (Häder *et al.* 1996; Hanelt *et al.* 1997; Gómez & Huovinen 2010). Higher phenolic contents in summer were previously reported for other fucoids including *Fucus vesiculosus* Linnaeus, *Himanthalia elongata* (Linnaeus) S. F. Gray and *Ascophyllum nodosum* (Linnaeus) Le Jolis (Connan *et al.* 2004). The highly dynamic variation of phenol contents in *D. antarctica* reinforces the idea that the adjustments in phlorotannin concentrations serve as effective photoprotection strategy.

Pigments also present dynamic changes over time in response to variations in solar radiation (López-Figueroa 1992; Aguirre-von-Wobeser *et al.* 2000; Huovinen *et al.* 2006). However, the observed daily photosynthetic performance in floating *Durvillaea antarctica* did not appear to be related to variations in concentrations of chlorophylls and total carotenoids. Photoacclimation through changes in photosynthetic pigment generally occurs over timescales of days to weeks (Long *et al.* 1994; Ralph & Gademann 2005) or seasons (Gevaert *et al.* 2002). However, rapid dynamic changes in accessory carotenoids such as fucoxanthin, zeaxanthin, violaxanthin or antheraxanthin can occur over timescales of minutes or less (Ralph & Gademann 2005). Although total carotenoids did not mirror the photosynthetic diurnal changes, variation in their specific composition could be operating, especially those associated with the xanthophyll cycle (Vershinin & Kamnev 1996; Gevaert *et al.* 2002), an important protection mechanism under light stress.

Photoinhibition and recovery of photosynthetic performance

Photodamage depends on the intensity and duration of radiation exposure, and longer exposure requires more time for recovery from photoinhibition (Häder *et al.* 2001). Although photoinhibition is a mechanism of photodefense occurring throughout the year, a notable reduction in recovery capacity was observed during the summer, especially in *Durvillaea antarctica* blades floating in a static position. During the remainder of the year both blade sides fully recovered by the next morning, indicating the direct relation-

ship between radiation dose and recovery potential. During *in situ* floating conditions, a decrease in the photosynthetic efficiency of *D. antarctica* was observed with increasing floating time (Graiff *et al.* 2013; Tala *et al.* 2016). Photoacclimation also occurred in benthic *D. antarctica* and a photoinhibition of 50% was reached in full solar radiation, which required at least 7 h to recover completely (Gómez & Huovinen 2011).

The particular morphology of *Durvillaea antarctica* with a highly buoyant, large blade generates specific conditions for floating. If the floating kelp is turned over continuously, e.g. by wave action, both sides of the blade are able to maintain a high recovery capacity. Irregular and fluctuating patterns of light can mitigate the negative effect of photoinhibition, allowing activation of photoprotective mechanisms that favour photosynthetic recovery (Dromgoole 1987; Greene & Gerard 1990; Wing & Patterson 1993; Roleda & Dethleff 2011). Recovery of photosynthesis after a photoinhibitory event decreases at high temperature (Hanelt *et al.* 1992; Bruhn & Gerard 1996; Cruces *et al.* 2013). This relationship reinforces the idea of negative effects during summer (combination of high solar radiation and temperature) on photosynthetic performance, compromising the persistence of floating seaweeds. In this sense, the recovery potential of floating kelps would depend on the environmental conditions that kelp rafts face at the sea surface (e.g. sunny vs cloudy days, winter vs summer, intense seawater movement and splashing vs calm sea conditions).

UVR has been described as an important factor that affects the physiological performance of seaweeds mostly on intertidal shores (Huovinen *et al.* 2006; Gao & Xu 2010). Although UVR had only minor effect on the daily cycle of F_v/F_m, the recovery capacity was enhanced in floating kelps that were only exposed to PAR. Relatively small effects of UVR were described in seaweeds that are confronted with high radiation levels in their natural environment, where PAR inhibition on sunny days can mask or add to the UVR effects (Hanelt & Roleda 2009). Long recovery periods may be necessary in UVR-induced photoinhibition (Hanelt *et al.* 1993), which can explain the difference in recovery levels between both radiation treatments. Although blade side itself had no effect on recovery in the UVR cycle, the high recovery capacity of the sunny blade side compared with the other daily cycles underlines the importance of daily radiation dose (which was shorter in the UVR cycle due to shading after 2:00 PM) in the photobiological response of floating kelps.

Implications of environmental conditions for rafting dispersal potential

In their benthic environment attached *Durvillaea antarctica* are moved by strong wave action, and blades are continuously turned over, causing an irregular light pattern on the thallus. In littoral habitats, some seaweeds can efficiently use light-pulses under fluctuating high light conditions with positive effects on overall productivity (Greene & Gerard 1990; Wing *et al.* 1993). When bull kelps are detached and float at the sea surface, they still move with the waves, but under moderate wave conditions they are no longer turned over, resulting in overexposure of one blade side to solar radiation. This effect is detrimental for the floating bull kelps, ultimately compromising the floating persistence, especially during the summer

(Graiff *et al.* 2013). The shadow side of the blade receives mainly scattering and reflection radiation, resulting in higher levels of photosynthesis than observed on the sunny side of the blade. Possible translocation of organic compounds (Raven 2003; Gómez *et al.* 2007) between blade sides can occur to sustain sunny-side demands. Medullary filaments like sieve elements of Laminariales have been described in some Fucales (Roberts 1979; Moss 1983) as an anatomical system through which metabolite translocation can occur.

Along the coastal zone of central Chile, stronger winds occur in spring/summer, whereas in autumn/winter the winds are less intense, with a daily cycle of strong winds between 10:00 AM and 11:00 PM (Narváez *et al.* 2004). Thus, winds are strongest during the season and time of day with the highest solar radiation, facilitating the turnover of floating kelps and seawater splashing. These typical upwelling winds may not only cause floating kelps to tumble frequently, but also bring cooler waters to the sea surface (Aguirre *et al.* 2012), thereby possibly mitigating the negative impacts of solar radiation and high sea-surface temperatures during the summer and midday.

In conclusion, floating *Durvillaea antarctica* exhibit dynamic responses in photosynthetic performance and phlorotannin contents during the day. These are maintained across seasons with a high recovery capacity, regardless of the photoinhibition reached. Various factors can affect the persistence of floating seaweeds at the sea surface, such as the intensity of solar radiation (Huovinen *et al.* 2006; Graiff *et al.* 2013), sea-surface temperatures (Powles 1984; Rothäusler *et al.* 2011a, b), grazing of organisms associated with kelp rafts (Cerda *et al.* 2009), wave movements and UVR (this study). In the study area (at the equatorward distribution limit of *D. antarctica*), under certain conditions the capacity to recover from photobiological stress appears to be compromised, resulting in photodamage, which ultimately can lead to reduced floating persistence and dispersal potential. Since kelps at the northern population range acclimated to conditions at the sea surface during most of the year, it is considered most likely that *D. antarctica* from central and southern Chile will survive the floating conditions even better, because the environmental conditions (temperature, solar radiation) are more moderate than at lower latitudes. This implies that *D. antarctica* has an overall high floating potential throughout its distribution range. However, examining seasonal variations in photoacclimation processes, growth and reproduction over the latitudinal range of *D. antarctica* could help to better estimate the floating persistence of this rafting kelp and evaluate the importance of rafting for population connectivity of *D. antarctica* and its associated biota.

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SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at http://dx.doi.org/10.2216/16-93.1.s1.

REFERENCES

ABDALA-DÍAZ R.T., CABELLO-PASINI A., PÉREZ-RODRÍGUEZ E, CONDE ÁLVAREZ R.M. & FIGUEROA F.L. 2006. Daily and seasonal variations of optimum quantum yield and phenolic compounds in *Cystoseira tamariscifolia* (Phaeophyta). *Marine Biology* 148: 459–465.

ABDALA-DÍAZ R.T., CABELLO-PASINI A., MÁRQUEZ-GARRIDO E. & LÓPEZ FIGUEROA F. 2014. Intra-thallus variation of phenolic compounds, antioxidant activity, and phenolsulphatase activity in *Cystoseira tamariscifolia* (Phaeophyceae) from southern Spain. *Ciencias Marinas* 40: 1–10.

AGUIRRE C., PIZARRO O., STRUB P.T., GARREAUD R. & BARTH J.A. 2012. Seasonal dynamics of the near-surface alongshore flow off central Chile. *Journal of Geophysical Research* 117(C01006): 17 pp. doi: 10.1029/2011JC007379.

AGUIRRE-VON-WOBESER E., FIGUEROA F.L. & CABELLO-PASINI A. 2000. Effects of the UV radiation on photoinhibition of marine macrophytes in culture systems. *Journal of Applied Phycology* 12: 159–168.

BATES D., MAECHLER M., BOLKER B. & WALKER S. 2014. lme4: linear mixed-effects models using Eigen and S4. R package, version 1.1-7.

BEARHAM D., VANDERKLIFT M.A. & GUNSON J.R. 2013. Temperature and light explain spatial variation in growth and productivity of the kelp *Ecklonia radiata*. *Marine Ecology Progress Series* 476: 59–70.

BISCHOF K., HANELT D., TÜG H., KARSTEN U., BROUWER P.E.M. & WIENCKE C. 1998. Acclimation of brown algal photosynthesis to ultraviolet radiation in Arctic coastal waters (Spitsbergen, Norway). *Polar Biology* 20: 388–395.

BRUHN J. & GERARD V.A. 1996. Photoinhibition and recovery of the kelp *Laminaria saccharina* at optimal and superoptimal temperatures. *Marine Biology* 125: 639–648.

CABELLO-PASINI A., AGUIRRE-VON-WOBESER E. & FIGUEROA F.L. 2000. Photoinhibition of photosynthesis in *Macrocystis pyrifera* (Phaeophyceae), *Chondrus crispus* (Rhodophyceae) and *Ulva lactuca* (Chlorophyceae) in outdoor culture systems. *Journal of Photochemistry and Photobiology B: Biology* 57: 169–178.

CERDA O., KARSTEN U., ROTHÄUSLER E., TALA F. & THIEL M. 2009. Compensatory growth of the kelp *Macrocystis integrifolia* (Phaeophyceae, Laminariales) against grazing of *Peramphitoe femorata* (Amphipoda, Amphitoidae) in northern-central Chile. *Journal of Experimental Marine Biology and Ecology* 377: 61–67.

COLLANTES G., MERINO A. & LAGOS V. 2002. Fenología de la gametogénesis, madurez de conceptáculos, fertilidad y embriogénesis en *Durvillaea antarctica* (Chamisso) Hariot (Phaeophyta, Durvillaeales). *Revista de Biologia Marina y Oceanografia* 37: 83–112.

CONNAN S., GOULARD F., STIGER V., DESLANDES E. & AR GALL E. 2004. Interspecific and temporal variation in phlorotannin levels in an assemblage of brown algae. *Botanica Marina* 47: 410–416.

CONNAN S., DESLANDES E. & AR GALL E. 2007. Influence of day–night and tidal cycles on phenol content and antioxidant capacity in three temperate intertidal brown seaweeds. *Journal of Experimental Marine Biology and Ecology* 349: 359–369.

CRUCES E., HUOVINEN P. & GÓMEZ I. 2012. Phlorotannin and antioxidant responses upon short-term exposure to UV radiation and elevated temperate in three South Pacific kelps. *Photochemistry and Photobiology* 88: 58–66.

CRUCES E., HUOVINEN P. & GÓMEZ I. 2013. Interactive effects of UV radiation and enhanced temperature of photosynthesis, phlorotannin induction and antioxidant activities of two sub-Antarctic brown algae. *Marine Biology* 160: 1–13.

DROMGOOLE F.I. 1987. Photosynthesis of marine algae in fluctuating light. I. Adjustment of rate in constant and fluctuating light regimes. *Functional Ecology* 1: 377–386.

EDWARDS M.S. & KIM K.Y. 2010. Diurnal variation in relative photosynthetic performance in giant kelp *Macrocystis pyrifera* (Phaeophyceae, Laminariales) at different depths as estimated using PAM fluorometry. *Aquatic Botany* 92: 119–128.

FRASER C.I., WINTER D.J., SPENCER H.G. & WATERS J.M. 2010. Multigene phylogeny of the southern bull-kelp genus *Durvillaea* (Phaeophyceae: Fucales). *Molecular Phylogenetics and Evolution* 57: 1301–1311.

GAO K. & XU J. 2010. Ecological and physiological responses of macroalgae to solar and UV radiation. In: *Seaweeds and their role in globally changing environments, cellular origin, life in extreme habitats and astrobiology* (Ed. By J. Seckbach, R. Einav & A. Israel). pp. 183–198. Springer Science+Business Media B.V. 15.

GAO X., ENDO H., MICHIKO NAGAKI M. & AGATSUMA Y. 2017. Interactive effects of nutrient availability and temperature on growth and survival of different size classes of *Saccharina japonica* (Laminariales, Phaeophyceae. *Phycologia*. In press.

GEVAERT F., CREACH A., DAVOULT D., HOLL A.-C., SEURONT L. & LEMOINE Y. 2002. Photo-inhibition and seasonal photosynthetic performance of the seaweed *Laminaria saccharina* during a simulated tidal cycle: chlorophyll fluorescence measurements and pigment analysis. *Plant, Cell and Environment* 25: 859–872.

GÓMEZ I. & HUOVINEN P. 2010. Induction of phlorotannins during UV exposure mitigates inhibition of photosynthesis and DNA damage in the kelp *Lessonia nigrescens*. *Photochemistry and Photobiology* 86: 1056–1063.

GÓMEZ I. & HUOVINEN P. 2011. Morpho-functional patterns and zonation of South Chilean seaweeds: the importance of photosynthetic and bio-optical traits. *Marine Ecology Progress Series* 422: 77–91.

GÓMEZ I., LÓPEZ-FIGUEROA F., ULLOA N., MORALES V., LOVENGREEN C., HUOVINEN P. & HESS S. 2004. Patterns of photosynthesis in 18 species of intertidal macroalgae from southern Chile. *Marine Ecology Progress Series* 270: 103–116.

GÓMEZ I., OROSTEGUI M. & HUOVINEN P. 2007. Morpho-functional patterns of photosynthesis in the south pacific kelp *Lessonia nigrescens*: effects of UV radiation on ^{14}C fixation and primary photochemical reactions. *Journal of Phycology* 43: 55–64.

GRAIFF A., KARSTEN U., MEYER S., PFENDER D., TALA F. & THIEL M. 2013. Seasonal variation in floating duration of *Durvillaea antarctica* (Chamisso) Hariot at their northern distribution limit in the SE Pacific. *Botanica Marina* 56: 3–14.

GREENE R.M. & GERARD V.A. 1990. Effects of high-frequency light fluctuations on growth and photoacclimation of the red alga *Chondrus crispus*. *Marine Biology* 105: 337–344.

HÄDER D.P. & FIGUEROA F.L. 1997. Photoecophysiology of marine macroalgae. *Photochemistry and Photobiology* 66: 1–14.

HÄDER D.P., HERRMANN H. & SANTAS R. 1996. Effects of solar radiation and solar deprived of UV-B and total UV on photosynthetic oxygen production and pulse amplitude modulated fluorescence in the brown alga *Padina pavonica*. *FEMS Micriobiology Ecology* 19: 53–61.

HÄDER D.P, PORST M. & LEBERT M. 2001. Photosynthetic performance of the Atlantic brown macroalgae, *Cystoseira abies-marina*, *Dictyota dichotoma* and *Sargassum bulgare*, measured in Gran Canaria on site. *Environmental and Experimental Botany* 45: 21–32.

HANELT D. & ROLEDA M.Y. 2009. UVB radiation may ameliorate photoinhibition in specific shallow-water tropical marine macrophytes. *Aquatic Botany* 91: 6–12.

HANELT D., HUPPERTZ K. & NULTSCH W. 1992. Photoinhibition of photosynthesis and its recovery in red algae. *Botanica Acta* 105: 227–342.

HANELT D., HUPPERTZ K. & NULTSCH W. 1993. Daily course of photosynthesis and photoinhibition in marine macroalgae investigated in the laboratory and field. *Marine Ecology Progress Series* 97: 31–37.

HANELT D., MELCHERSMANN B., WIENCKE C. & NULTSCH W. 1997. Effects of high light stress on photosynthesis of polar macroalgae in relation to depth distribution. *Marine Ecology Progress Series* 149: 255–266.

HENLEY W.J. & DUNTON K.H. 1995. A seasonal comparison of carbon, nitrogen, and pigment content in *Laminaria solidungula* and *L. saccharina* (Phaeophyta) in the Alaskan Arctic. *Journal of Phycology* 31: 325–331.

HERNÁNDEZ-CARMONA G., HUGHES B. & GRAHAM M. 2006. Reproductive longevity of drifting kelp *Macrocystis pyrifera* (Phaeophyceae) in Monterey Bay, USA. *Journal of Phycology* 42: 1199–1207.

HINOJOSA I.A., PIZARRO M., RAMOS M. & THIEL M. 2010. Spatial and temporal distribution of floating kelp in the channels and fjords of southern Chile. *Estuarine, Coastal and Shelf Science* 87: 367–377.

HOBDAY A.J. 2000. Age of drifting *Macrocystis pyrifera* (L.) C. Agardh rafts in the Southern California Bight. *Journal of Experimental Marine Biology and Ecology* 253: 97–114.

HUOVINEN P., GÓMEZ I. & LOVENGREEN C. 2006. A five-year study of solar ultraviolet radiation in southern Chile (39°S): potential impact on physiology of coastal marine algae? *Photochemistry and Photobiology* 82: 515–522.

HURD C.L., HARRISON P.J., BISCHOF K. & LOBBAN C.S. 2014. Seaweed Ecology and Physiology. Cambridge University Press, Cambridge, United Kingdom. Second ed.

INSKEEP W.P. & BLOOM P.R. 1985. Extinction coefficients of chlorophyll *a* and *b* in *N*, *N*-dimetylformamide and 80% acetone. *Plant Physiology* 77: 483–485.

KIM S. & CHOI W. 2005. Visible-light-induced photocatalytic degradation of 4-chlorophenol and phenolic compounds in aqueous suspension of pure titania: demonstrating the existence of a surface-complex-mediated path. *Journal of Physical Chemistry B* 109: 5143–5149.

KOKUBU S., NISHIHARA G.N., WATANABE Y., TSUCHIYA Y., AMAMO Y. & TERADA R. 2015. The effect of irradiance and temperature on the photosynthesis of a native alga *Sargassum fusiforme* (Fucales) from Kagoshima, Japan. *Phycologia* 54: 235–247.

LIZÉE-PRYNNE D., LÓPEZ B., TALA F. & THIEL M. 2016. No sex-related dispersal limitation in a dioecious, oceanic long-distance traveller: the bull kelp *Durvillaea antarctica*. *Botanica Marina* 59: 39–50.

LONG S.P., HUMPHRIES S. & FALKOWSKI P.G. 1994. Photoinhibition of photosynthesis in nature. *Annual Review of Plant Physiology and Plant Molecular Biology* 45: 633–662.

LÓPEZ B., MACAYA E., TELLIER F., TALA F. & THIEL M. 2016. The variable routes of rafting: stranding dynamics of floating bull-kelp *Durvillaea antarctica* (Fucales, Phaeophyceae) on beaches in the SE Pacific. *Journal of Phycology*, doi: 10.1111/jpy.12479.

LÓPEZ-FIGUEROA F. 1992. Diurnal variation in pigment content in *Porphyra laciniata* and *Chondrus crispus* and its relation to the diurnal changes of underwater light quality and quantity. *Marine Ecology* 13: 285–305.

LÜNING K. & TOM DIECK I. 1989. Environmental triggers in algal seasonality. *Botanica Marina* 32: 389–397.

MOSS B.L. 1983. Sieve elements in the Fucales. *New Phytologist* 93: 433–438.

NARVÁEZ D.A., POULIN E., LEIVA G., HERNÁNDEZ E., CASTILLA J.C. & NAVARRETE S.A. 2004. Seasonal and spatial variation of nearshore hydrographic conditions in central Chile. *Continental Shelf Research* 24: 279–292.

POWLES S.B. 1984. Photoinhibition of photosynthesis induced by visible light. *Annual Review of Plant Physiology* 35: 15–44.

QUINN P. & KEOUGH M.J. 2002. *Experimental design and data analysis for Biologists*. Cambridge University Press, Cambridge, UK. 556 pp.

R CORE TEAM. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RALPH P. & GADEMANN R. 2005. Rapid light curves: a powerful tool to assess photosynthetic activity. *Aquatic Botany* 82: 222–237.

RAVEN J.A. 2003. Long-distance transport in non-vascular plants. *Plant, Cell and Environment* 26: 73–85.

ROBERTS M. 1979. Observations on cell structure and cytology of the genus *Durvillaea* Bory. *New Zealand Journal of Botany* 17: 241–249.

ROLEDA M.Y. & DETHLEFF D. 2011. Storm-generated sediment deposition on rocky shores: simulating burial effects on the

physiology and morphology of *Saccharina latissima* sporophytes. *Marine Biology Research* 7: 213–223.

ROLEDA M.Y., HANELT D. & WIENCKE C. 2006. Exposure to ultraviolet radiation delays photosynthetic recovery in arctic kelp zoospores. *Photosynthesis Research* 88: 311–322.

ROTHÄUSLER E., GÓMEZ I., KARSTEN U., TALA F. & THIEL M. 2011a. Physiological acclimation of floating *Macrocystis pyrifera* to temperature and irradiance ensures long-term persistence at the sea surface at mid-latitudes. *Journal of Experimental Marine Biology and Ecology* 405: 33–41.

ROTHÄUSLER E., GÓMEZ I., HINOJOSA I.A., KARSTEN U., MIRANDA L., TALA F. & THIEL M. 2011b. Kelp rafts in the Humboldt Current: interplay of abiotic and biotic factors limit their floating persistence and dispersal potential. *Limnology and Oceanography* 56: 1751–1763.

ROTHÄUSLER E., GÓMEZ I., HINOJOSA I.A., KARSTEN U., TALA F. & THIEL M. 2011c. Physiological performance of floating giant kelp *Macrocystis pyrifera* (Phaeophyceae): latitudinal variability in the effects of temperature and grazing. *Journal of Phycology* 47: 269–281.

SILVA J. & SANTOS R. 2003. Daily variation patterns in seagrass photosynthesis along a vertical gradient. *Marine Ecology Progress Series* 257: 37–44.

SMITH S.D.A. 2002. Kelp rafts in the Southern Ocean. *Global Ecology and Biogeography* 11: 67–69.

STEINHOFF F.S., WIENCKE C., WUTTKE S. & BISCHOF K. 2011. Effects of water temperatures, UV radiation and low vs high PAR on phlorotannin content and germination in zoospores of *Saccorhiza dermatodea* (Tilopteridales, Phaeophyceae). *Phycologia* 50: 256–263.

STEVENS C.L., HURD C.L. & SMITH M.J. 2002. Field measurement of the dynamics of the bull kelp *Durvillaea antarctica* (Chamisso) Heriot. *Journal of Experimental Marine Biology and Ecology* 269: 147–171.

SWANSON A.K. & DRUEHL L.D. 2002. Induction, exudation and the UV protective role of kelp phlorotannins. *Aquatic Botany* 73: 241–253.

TALA F., GÓMEZ I., LUNA-JORQUERA G. & THIEL M. 2013. Morphological, physiological and reproductive conditions of rafting bull kelp (*Durvillaea antarctica*) in northern-central Chile (30°S). *Marine Biology* 160: 1339–1351.

TALA F., VELÁSQUEZ M., MACAYA E., MANSILLA A. & THIEL M. 2016. Latitudinal and seasonal effects on short-term acclimation of floating kelp species from the South-East Pacific. *Journal of Experimental Marine Biology and Ecology* 483: 31–41.

TERADA R., SHIKADA S., WATANABE Y., NAKAZAKI Y., MATSUMOTO K., KOZONO J., SAINO N. & NISHIHARA G.N. 2016. Effect of PAR and temperature on the photosynthesis of the Japanese alga, *Ecklonia radicosa* (Laminariales), based on field and laboratory measurements. *Phycologia* 55: 178–186.

VAN ALSTYNE K.L., MCCARTHY J.J. III, HUSTEAD C.L. & DUGGINS D.O. 1999. Geographic variation in polyphenolic levels of Northeastern Pacific kelps and rockweeds. *Marine Biology* 133: 371–379.

VANDENDRIESSCHE S., VINCX M. & DEGRAER S. 2007. Floating seaweed and the influences of temperature, grazing and clump size on raft longevity – a microcosm study. *Journal of Experimental Marine Biology and Ecology* 343: 64–73.

VERSHININ A.O. & KAMNEV A.N. 1996. Xanthophyll cycle in marine macroalgae. *Botanica Marina* 39: 421–425.

WICHMANN C.S., HINOJOSA I.A. & THIEL M. 2012. Floating kelps in Patagonian Fjords: an important vehicle for rafting invertebrates and its relevance for biogeography. *Marine Biology* 159: 2035–2049.

WING S.R. & PATTERSON M.R. 1993. Effects of wave-induced lightflecks in the intertidal zone on photosynthesis in the macroalgae *Postelsia palmaeformis* and *Hedophyllum sessile* (Phaeophyceae). *Marine Biology* 116: 519–525.

WING S.R., LEICHTER J.J. & DENNY M.W. 1993. A dynamic model for wave-induced light fluctuations in a kelp forest. *Limnology and Oceanography* 38: 396–407.