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Morphological, physiological and reproductive conditions of rafting bull kelp (*Durvillaea antarctica*) in northern-central Chile (30°S)

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Abstract The bull kelp *Durvillaea antarctica* is a common floating alga in the southern hemisphere, but despite the ecological and biogeographic importance of kelp rafts, little is known about the responses of detached kelps to the conditions at the sea surface. The morphological, physiological and reproductive performances of *D. antarctica* rafts in the Coastal System of Coquimbo, Chile (CSC, ~30°S), were examined during winter and summer of two successive years (2010/11 and 2011/12). Epibionts (*Lepas* spp.) that only attach to floating objects were used as indicator for the floating time of kelp rafts. Photosynthetic efficiency and reproductive maturity of both benthic and floating algae varied seasonally, with a stronger decrease in summer than in winter. Blade size (measured as weight proportion of kelp individuals), phlorotannin concentrations and antioxidant activities were lower in floating than in benthic algae. Environmental conditions and floating time affected the blade tissues, with stronger negative effects during summer. These results confirm that floating persistence of *D. antarctica* in the CSC is suppressed during the summer months, which indicates that the dispersal potential of this (and other) floating algae varies seasonally.

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Introduction

Floating macroalgae are important dispersal agents for a wide diversity of associated organisms and for the algae themselves (Hobday 2000a; Thiel and Gutow 2005a; Vandendriessche et al. 2006; Rothäusler et al. 2012). The dispersal potential of algal rafts depends on supply from source populations and the persistence time at the sea surface. Some brown algae survive for extended time periods (weeks–months) after detachment (Hobday 2000b; Hernández-Carmona et al. 2006), but during unfavorable environmental conditions, they degrade and sink rapidly (Vandendriessche et al. 2007; Rothäusler et al. 2009).

At the sea surface, floating algae are exposed to a variety of environmental factors that differ from those in benthic habitats. For example, while benthic algae are well adapted to cope with high light levels during spring and summer (Lüning 1990; Huovinen et al. 2006; Dethier et al. 2009), physiological acclimation of floating algae can be strongly impaired by increased levels of solar radiation and higher temperature at the sea surface (e.g., Hobday 2000a; Vandendriessche et al. 2007; Rothäusler et al. 2009, 2011a, b, c).

Seasonal variations in the abundances of algal rafts have been recorded in particular areas (Yoshida 1963; Hirata et al. 2001; Hinojosa et al. 2010). In most cases higher abundances of floating algae were detected during spring–summer (Hinojosa et al. 2010; 2011; Thiel et al. 2011;

Wichmann et al. 2012), associated with high supply from benthic populations resulting from intense recruitment and growth during the spring months. However, during summer, temperature and solar radiation are high, possibly limiting the dispersal potential of floating algae. In contrast, during winter the floating populations might be small, but detached algae might float for longer time periods (and over longer distances) under more favorable environmental conditions (low temperature and moderate solar radiation). Since brown algae (including common floating algae) from temperate regions are susceptible to strong solar radiation and high water temperatures (Lüning 1990; Graham et al. 2007), we hypothesize that persistence at the sea surface is restricted during the summer season.

Most studies on growth, reproduction and physiology of floating algae at the sea surface so far have focused on the giant kelp *Macrocystis pyrifera* (e.g., Hobday 2000a; Macaya et al. 2005; Rothäusler et al. 2009, 2011a, d). However, the bull kelp *Durvillaea antarctica* (Chamisso) Hariot is frequently found floating in the subantarctic (Smith 2002) and cold-temperate regions of the southern hemisphere (Smith 2002; Waters 2008; Hinojosa et al. 2010; Wichmann et al. 2012). *Durvillaea antarctica* can reach >10 m length, and typical holdfasts may comprise several stipes (Santelices et al. 1980; Hay 1994). The medullar tissue with the gas-filled honeycomb structure within the blade (palm) provides strength and high buoyancy and also can be offering protection against potential damage by the strong waves in its natural habitat (Santelices et al. 1980; Hay 1994; Koehl 1999). On the other hand, the buoyancy of the lamina in this species has important implications for UV and thermal stress tolerance (Cruces et al. 2012, 2013). When an individual of *D. antarctica* is detached, the raft functional unit is composed mainly of the holdfast, one or several stipes and blades of different sizes. While holdfasts comprising several stipes might be composed of genetically different individuals (stipes), the floating capacity of the holdfast depends on the ability to respond as a functional unit to the condition at the sea surface. While floating, almost the entire blade floats at the sea surface, where it is directly exposed to solar radiation and aerial conditions. Here, the capacity to acclimate or to resist the new environmental conditions is a key factor determining the potential dispersal distances of the rafts.

Along the Chilean coast, benthic populations of *D. antarctica* occur between 30°S (Coquimbo) and 56°S (Cape Horn). This kelp grows in the low intertidal zone of exposed rocky shores where it commonly cohabits with the non-buoyant kelp *Lessonia nigrescens* (Santelices et al. 1980; Westermeier et al. 1994; Hoffmann and Santelices 1997; Collantes et al. 2002). Molecular studies confirm the existence of two genetically differentiated clades of *D. antarctica* in Chile (Fraser et al. 2009). Phylogenetic analyses revealed high levels of genetic differentiation among the Chilean populations of *D. antarctica* (Fraser et al. 2010a). Genetic homogeneity is found in the populations from southern Chile (south of 46°S); this clade is also distributed throughout the entire subantartic region (Fraser et al. 2009). The populations from central Chile (30°S–46°S) represent a genetically differentiated clade that (based on the genetic divergence from the subantarctic clade) should be recognized as a separate species (Fraser et al. 2010a, b). The subantarctic clade found in southern Chile has a high potential for long-distance dispersal (Fraser et al. 2009), while the dispersal potential of the clade from central Chile appears to be limited (Fraser et al. 2010b). These variations in realized dispersal might be due to differences in the acclimation potential between these two clades. Therefore, it is important to understand the ecophysiological responses of *D. antarctica* to the floating conditions.

Notwithstanding the ecological and biogeographic importance of *D. antarctica,* little is known about its morphological and physiological responses to the conditions at the sea surface. In particular, the effects of seasonally variable conditions on the performance of floating kelps have not been examined. A previous study on *Macrocystis* rafts across a latitudinal gradient showed that epibiont cover and size increased with distances from potential sources, while morphometric traits (blade length, biomass distribution), physiological indicators and reproductive performance decreased (Rothäusler et al. 2011d). That study was done only during summer, when environmental conditions, especially high temperatures and solar radiation, are hypothesized to limit the dispersal potential of kelp rafts more drastically than during winter conditions. In order to test this hypothesis, herein we determined the morphological (size, length), physiological (photosynthesis, pigments and phlorotannin contents as well as antioxidant activity) and reproductive (conceptacle maturity) traits of *D. antarctica* rafts in the Coastal System of Coquimbo (CSC) in contrasting seasons (winter and summer) during two consecutive years. We also examined whether these traits were related to the condition of algae (benthic or floating) and approximate floating times, using epibionts (*Lepas* spp.) as a proxy for floating time. It was predicted that kelp rafts with larger epibionts (indicating longer floating times) had lower physiological performance and stronger signs of degradation than rafts without epibionts or benthic kelps.

Materials and methods

Study area

Algae were sampled in the Coastal System of Coquimbo (CSC) along the northern-central coast of Chile (Fig. 1).

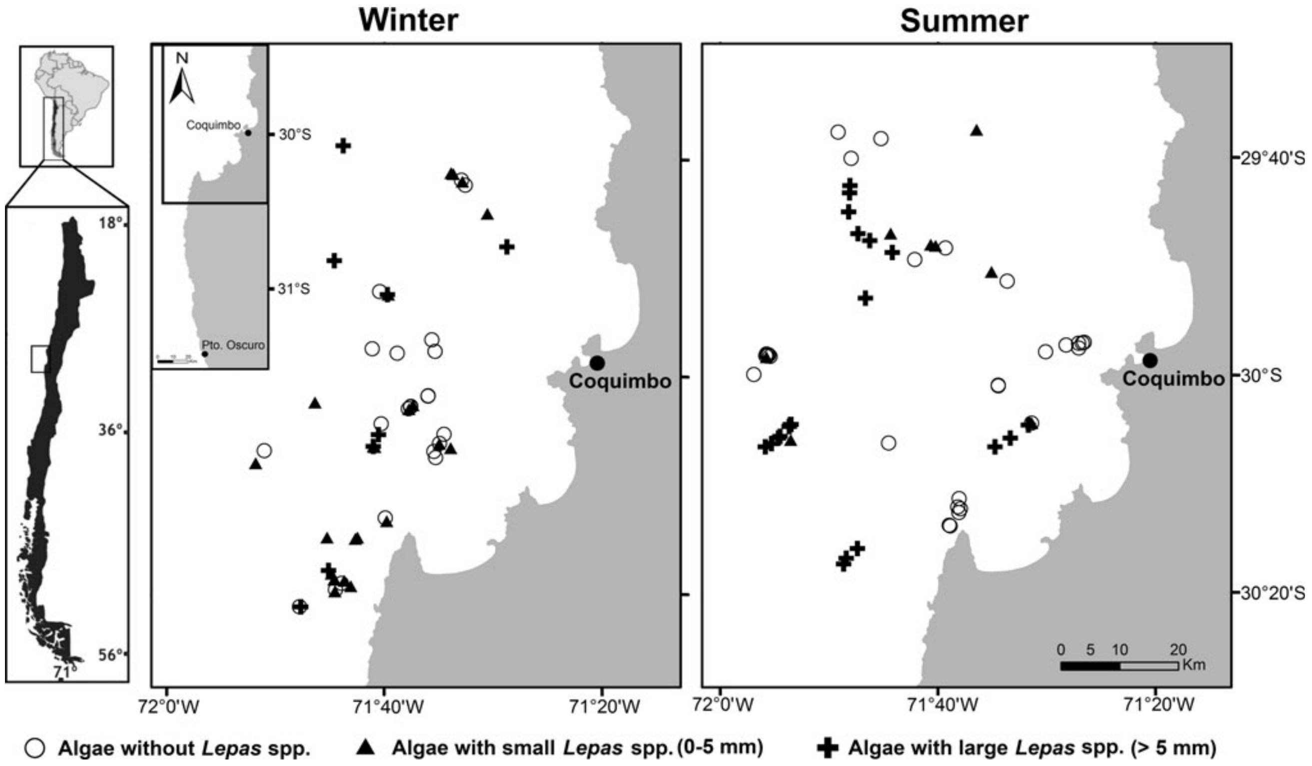

Fig. 1 Study area and spatial distribution of the floating and benthic *D. antarctica* in the Coastal System of Coquimbo (CSC) during sampling period

The CSC extends from Punta Lengua de Vaca (30°17′S, 71°36′W) in the south up to Punta de Choros (29°14′S, 71°28′W) in the north. Benthic source populations of *D. antarctica* occur only to the south of the CSC, which also corresponds to the northern edge of the geographic distribution of this species (Hoffmann and Santelices 1997). Within the CSC, *D. antarctica* can often be found floating and rafts generally pass the system in a northward direction. This region is under the influence of the coastal branch of the Humboldt Current System, with surface currents generally moving toward the north (equatorward) driven by usually southern wind (Marín and Delgado 2007; Rahn et al. 2012). Two upwelling zones close to Punta Lengua de Vaca and Punta de Choros are identified within this bay system (Rutllant and Montecino 2002).

Throughout the course of the study, incident UVB and UVA radiations were monitored using UV3pB (290–340 nm) and UV3pA (340–400 nm) sensors (Delta-T Devices Ltd, Cambridge, UK) connected to a Li-Cor-1,400 data logger (Li-Cor Bioscience, Lincoln, NE, USA). As the UV ranges measured by the sensors differ slightly from those defined by the International Commission on Illumination (CIE), the UVB sensor can overestimate the UVB waveband (290–315 nm, CIE) and the UVA sensor can produce a corresponding underestimation (315–400 nm, CIE). In parallel, photosynthetically active radiation (PAR 400-700 nm) data were gathered with a LI-190SA quantum sensor. The sensors were placed free of physical interference, and ultraviolet and PAR were measured every 15 min throughout the day from 07:00 to 19:00. Surface water temperature was registered daily in Bahía La Herradura, Coquimbo, Chile (29°57′S, 71°20′W), within the CSC. Solar radiation and sea surface temperature followed a predictable seasonal pattern, with higher values during summer (Tables 1, S1). Solar radiation differed significantly between seasons (ANOVA, $P = 0.0001$). Sea surface temperatures were on average 3 °C higher during summer than during winter (ANOVA $P = 0.0001$, Tukey < 0.05) (Tables 1, S2).

Sampling of floating and benthic bull kelps

In order to determine the morphological, physiological and reproductive performance of floating *D. antarctica* in the field, natural kelp rafts were sampled in the CSC (Fig. 1). We exploited the fact that kelps detached south of Punta Lengua de Vaca generally move in a northward direction within the CSC (M. Thiel et al., unpublished data). The kelp rafts are defined as a functional unit composed of a holdfast and one or more stipe(s) and blade(s). The number of stipes per holdfast ranged from 1 to 13 for floating and 1–8 for benthic individuals (Fig. S1). Most holdfasts had

Table 1 Daily mean of environmental condition in (A) solar radiation (PAR 400–700-nm, UV A 340–400 nm and UV B 290–340 nm) and (B) seawater temperature during sampling seasons

	Winter 2010 4 days	Summer 2010/11 91 days	Winter 2011 65 days	Summer 2011/12 69 days
(A) Solar radiation				
PAR				
Range (μmol photon m^{-2} s^{-1})	619–886	508–1,380	165–912	386–1,379
Mean ± SD (μmol photon m^{-2} s^{-1})	731 ± 114	999 ± 212	585 ± 207	862 ± 262
UV A				
Range (W m^{-2})	25.7–40.8	42.0–112.4	11.0–75.6	24.5–121.4
Mean ± SD (W m^{-2})	34.5 ± 6.9	78.9 ± 17.8	48.0 ± 17.8	84.2 ± 24.4
UV B				
Range (W m^{-2})	1.2–2.0	1.3–4.5	1.0–2.3	1.0–4.4
Mean ± SD (W m^{-2})	1.6 ± 0.4	2.3 ± 0.5	1.6 ± 0.3	3.1 ± 0.9
(B) Temperature				
Mean ± SD	12.9 ± 0.5	17.1 ± 0.6	12.9 ± 0.4	17.2 ± 0.9
Min	12.1	15.9	12.1	15.6
Max	13.8	18.0	14.0	19.0

one to three stipes (76 % of the floating and 84 % of the benthic individuals). Rafts were collected along a south–north gradient (Fig. 1), during seasonal (winter and summer) ship surveys in two successive years (2010/11 and 2011/12). The sampling data were 28 August–12 September for winter 2010, 10–19 January for summer 2010–11, 5–25 July for winter 2011 and 4–24 January for summer 2011–12. The sampling time often depends on appropriate weather conditions, both for floating algae and for benthic algae on the exposed rocky shores inhabited by *D. antarctica*; therefore, the entire sampling period often extends over 2–3 weeks.

Rafts were sampled with a boat hook, immediately placed in a large tank filled with seawater (500 L) and covered with a dark mesh, so that all floating structures were always kept underwater or moist. When we encountered oceanic fronts where kelp rafts and other floating items had accumulated, we randomly sampled about eight *D. antarctica* rafts and recorded their position with a handheld GPS. The research vessel returned to port every night, where samples were kept overnight in a large outdoor flow-through tank (2,000 L) to be processed on the following day.

Samples from a benthic population (Puerto Oscuro, 31°25′S–71°36′W) about 150 km south of the sampling area were used as reference for the conditions of attached algae. This site is close to the northern edge of the geographic distribution of *D. antarctica*. Single individuals can also be found on exposed rocky shores north of Puerto Oscuro, but these are too scarce to serve as possible source populations for the numerous *D. antarctica* rafts found floating in the CSC. Similar as for the floating kelps, the benthic individuals were sampled randomly from the population in Pto. Oscuro. They were transported to the laboratory in a large tank with seawater and then kept overnight in a large outdoor flow-through tank (2,000 L) to be processed on the following day.

As changing environmental conditions can provoke differences in some physiological responses (Figueroa et al. 1997; Altamirano et al. 2000; Abdala-Díaz et al. 2006; Cruces et al. 2012), we applied the same procedures for benthic and floating kelps to standardize the measurements of physiological variables.

Categories of floating and benthic *D. antarctica* (algal status)

Herein, three different categories of kelp rafts were distinguished and compared with benthic *D. antarctica*. The categories of floating algae were based on the presence and sizes of the barnacle *Lepas* spp. All kelp rafts were examined for the presence of epibionts, and three subsamples were taken from holdfast, stipe and blade. Stalked barnacles (*Lepas* spp.) were removed, and the length of the capitulum was measured. The body size of stalked barnacles serves as a good proxy for minimum floating time (FT) because they are common on floating substrata but do not grow on attached algae (see also Macaya et al. 2005; Fraser et al. 2011). According to Thiel and Gutow (2005b), the capitulum of *Lepas anatifera* has a daily growth rate of 0.44 mm day^{-1} and that of *L. pectinata* is 0.37 mm day^{-1}. The main species found on floating *D. antarctica* during this study was *L. australis*. This species has an estimated daily growth rate of 0.46 mm day^{-1} (Skerman 1958). Considering the distribution and size range of *Lepas* found on floating bull kelp samples (min–max 1.05–14.27 mm), we estimated that *D. antarctica* with 5 mm *L. australis* had been afloat for at least 11 days. The samples with the largest *L. australis* in summer (12.22 mm) and winter (14.27 mm) found herein had thus floated for a minimum of 27–31 days, respectively.

For all statistical analyses, four categories of algae (termed "algal status" in the following) were used: benthic algae, floating algae with no *Lepas*, with small *Lepas* (0–5 mm) and with large *Lepas* (>5 mm). The size of 5 mm (representing 10–14 days of floating) to distinguish bull kelps floating for intermediate and long time periods was chosen, because previous studies with *M. pyrifera* had shown that important changes in algal physiology (and reproductive activity) occur within this time period (Rothäusler et al. 2009, 2011a, d).

Measurements of algal traits

For each algal sample, we measured the physiological performance based on photosynthetic parameters (chlorophyll *a*—Chl *a*, maximal quantum yield of chlorophyll fluorescence—F_v/F_m and maximal electron transport rate—ETR_{max}, from P–I curve). Furthermore, the antioxidant activity and soluble phlorotannin concentrations were determined. In addition, the biomass proportion of positively buoyant tissues (blade) and the reproductive stages were quantified.

Within-individual biomass distribution

In order to determine the wet biomass distribution of the different tissue components within a single individual, each alga was dissected into holdfast, stipe and blade. Algal parts were weighed (g) separately, and the wet weights of algal samples that had been taken for physiological analyses were added to the vegetative blade biomass. For the analyses (see details below) we considered only the blade biomass proportion because it usually represents more than 50 % of total weight and *D. antarctica* obtains its buoyancy from the gas-filled honeycomb medulla. We calculated the proportion of blade weight on the basis of the total wet weight. For those holdfasts that had more than one stipe, the longest stipe was used as principal stipe for all other analyses (photosynthesis, pigments, phlorotannins, antioxidants and reproductive status). In some cases, the individuals were incomplete or lacking the holdfast; for these individuals (37 out of the total of 151 samples), the blade biomass proportion could not be calculated (see also below).

Measurements of algal physiological performance

General procedure All physiological variables were measured for floating thalli collected during the field survey and for benthic algae ($n = 25$–36 floating algae, and $n = 8$ benthic algae per Season and Year). Tissue samples were taken with a cork borer from the blade of the main stipe of each alga. If necessary, samples were cleaned from epibionts with seawater. Blade samples for pigments, antioxidant activity and soluble phlorotannin contents were frozen in liquid nitrogen and stored at –80 °C until analysis. All procedures were done in similar ways as in the previous studies with floating *Macrocystis* (Rothäusler et al. 2011a, d) and are briefly described below.

Pigment, antioxidant activity and phlorotannins

Photosynthetic pigments (Chl *a*) were determined in three subsamples from each collected thallus. Measurements of pigment concentrations were based on extraction with N,N-dimethylformamide (DMF) for 24 h at 4 °C in darkness. The extinctions of the extract and the determination of Chl *a* concentrations were calculated as described in Rothäusler et al. (2011a) and expressed as mg per g wet weight. Other pigments (chl *c* and carotenoids) present in the extracts were not considered for the statistical analyses because they are correlated with Chl *a*.

The antioxidant activity was tested by the free radical 2,2-diphenyl-1-picrylhydrazyl (DPPH) scavenging method of Brand-Williams et al. (1995) as modified by Fukumoto and Mazza (2000) for a 96-well microplate. DPPH (150 μM) was prepared in 80 % methanol and mixed with 22 μL of algal extract. The absorbance was measured at 520 nm using Trolox (6-hydroxy-2,5,7,8-tetramethylchroman-2-carboxylic acid) as standard. The antiradical activity was defined as μg Trolox equivalent (TE) on a wet weight basis.

Soluble phlorotannins (Phl) were determined from algal material removed from the freezer and stored in silica gel to dry (dw). To determine the concentration of soluble phlorotannins, we used the Folin–Ciocalteu assay described by Gómez and Huovinen (2010) with a 96-well microplate. Purified phloroglucinol (Sigma Aldrich) was used as a standard. Algal samples of ~10 mg dw were homogenized with liquid nitrogen in a mortar. After adding 1 mL acetone (70 %), the extract was kept shaking overnight at 4 °C. After centrifuging (2,500 rpm, 10 min), 50 μL of supernatant was solubilized in 250 μL of dH_2O, 200 μL of 20 % $NaCO_3$ and 100 μL of 1 N Folin–Ciocalteu reagent. The samples were incubated for 45 min at room temperature in darkness and centrifuged at 5,000 rpm for 3 min, and the absorbance was read at 730 nm. The values were expressed as mg Phl g^{-1} dry weight.

Chlorophyll fluorescence measurements

In vivo chlorophyll *a* fluorescence of photosystem II (PSII), that is, the maximal quantum yield (F_v/F_m) and the electron transport rate (ETR), was measured with a portable pulse modulation fluorometer (PAM 2500, Walz, Effeltrich, Germany). To determine the maximal quantum yield (F_v/F_m), three subsamples were taken with a cork borer from the middle blade with honeycomb medulla. The samples were incubated for 20 min in the dark, and each side of each subsample was measured once. Mean values of the six measurements were used to calculate the average response for each alga. The maximal quantum yield represents a sensitive indicator of the photochemical potential of algae, which might be affected by high photon fluence rates or stress exposure in general.

Electron transport rates (ETRs) were estimated from the effective quantum yield (the Genty parameter; Φ_{PSII}) versus light curves, irradiating individual sample disks ($n = 3$ per plant) with increasing photon fluence rates of PAR (0–1,500 μmol photon m^{-2} s^{-1}) provided by a light-emitting diode (LED) lamp of the PAM device (Schreiber et al. 1994).

ETR was determined relating effective quantum yield (Φ_{PSII}) to the intensity of the actinic irradiance as follows:

$$\mathrm{ETR} = \Phi_{PSII} \times E \times A \times 0.8$$

where E is the incident irradiance of PAR and A the thallus absorptance. A factor close to 0.8 has been estimated for brown algae (Grzymski et al. 1997), representing the fraction of absorbed quanta directed to PSII that are required to assimilate one CO_2 molecule. Absorptance was determined by placing the algae on a cosine-corrected PAR sensor (LI-190SA, Lincoln, USA) and calculating the light transmission as:

$$A = 1 - E_t E_o^{-1}$$

where E_t is the irradiance below the alga (transmitted light) and E_o the incident irradiance. For defining the ETR parameters, a modified nonlinear function of Jassby and Platt (1976) was fitted:

$$\mathrm{ETR} = \mathrm{ETR}_{max} \times \tanh(\alpha \times E/\mathrm{ETR}_{max})$$

where ETR_{max} is the maximal ETR, tanh the hyperbolic tangent function, α (an indicator of the efficiency of the electron transport) the initial slope of the P–I curve and E the incident irradiance.

Reproductive stages of bull kelp

The maturity stage of the conceptacles was determined as described in Collantes et al. (2002). Histological observations from the central blade zone of each alga were used to determine the maturity stage of approximately 100 conceptacles per alga. The four maturity stages of conceptacles were vegetative (V), immature (I), mature (M) and senescent (S). Algae without any conceptacles were considered as vegetative, while conceptacles in initial stages of maturation were considered as immature. Mature conceptacles had fully developed gametes, while senescent conceptacles were empty. The reproductive stage of each alga was determined based on the maturity stage found in the majority of the conceptacles examined per alga. The sex of *D. antarctica*, which is a dioecious species, could only be identified for mature and occasionally for senescent algae.

Statistical analyses

Multivariate analysis of variance (MANOVA) was used to determine the effects of the factors considered in this study on the benthic and floating algae, the physiological responses and proportion of blade mass (Quinn and Keough 2002). The explanatory variables were Year (1–2), Season (summer and winter) and Algal status (benthic and floating algae with no *Lepas*, with small *Lepas* 0–5 mm and with large *Lepas* >5 mm), all of which were treated as fixed effects.

The multinormality of the response variables was marginally significant (Henze–Zirkler test, $P = 0.0457$), indicating some deviation from the MANOVA assumption of multivariate normality. Since MANOVA is sensitive to multivariate outliers, we examined them using the Mahalanobis distance, but no outliers were observed. Conservatively, we also excluded the three-factor interactions. Although we maintain the significance level at the standard 0.05, the probability associated with the multivariate test was lower than 0.01, as recommended by Underwood (1997) when assumptions were not fulfilled. Besides, the multivariate tests are sufficiently robust to sustain some violation of the assumptions (Quinn and Keough 2002). Thus, while we found some deviation from the assumption of MANOVA, we are confident that the analysis is sufficiently robust to deal with it. The frequency of the maturity stage of algae across the factors was analyzed applying a log-linear model analysis (Quinn and Keough 2002). Starting from a saturated model, we simplified it gradually to determine the factors that have significant effects. All analyses were done using SYSTAT v.13 (Systat Software Inc., Chicago, USA).

Results

Rafts of *D. antarctica* were collected throughout the CSC; both in winter and in summer, rafts without epibionts as well as rafts with large *Lepas* spp. occurred in the entire study area (Fig. 1). The morphometry, physiological performance and reproductive stages differed between benthic and floating *D. antarctica*, and important differences were observed between summer and winter (Figs. 2–4). We detected highly significant effects of the Year, Season and Algal status on the response variables, both for single factors and for the two-factor interactions (MANOVA $P < 0.005$, see Tables 2, S3).

Blade biomass

In *D. antarctica* rafts, the biomass was dominated by the blade tissue, which usually made up 60–80 % of the entire raft biomass (Fig. 2a). The total biomass from benthic and floating kelps was log-normally distributed (Shapiro–Wilks test, $P = 0.269$). The log-transformed biomass values of *D. antarctica* were significantly different both between the Years (Year 2 > Year 1) and Algal status (small *Lepas* > benthic > large *Lepas* > without *Lepas*), but not between Seasons (Table S4). Also, the mean of transformed biomass values was significantly affected by the interaction between Season and Algal status, but not by the interaction between Season and Year (factorial ANOVA, $P < 0.005$; Table S4). Seasonal differences were detected only for floating algae with small and large *Lepas*.

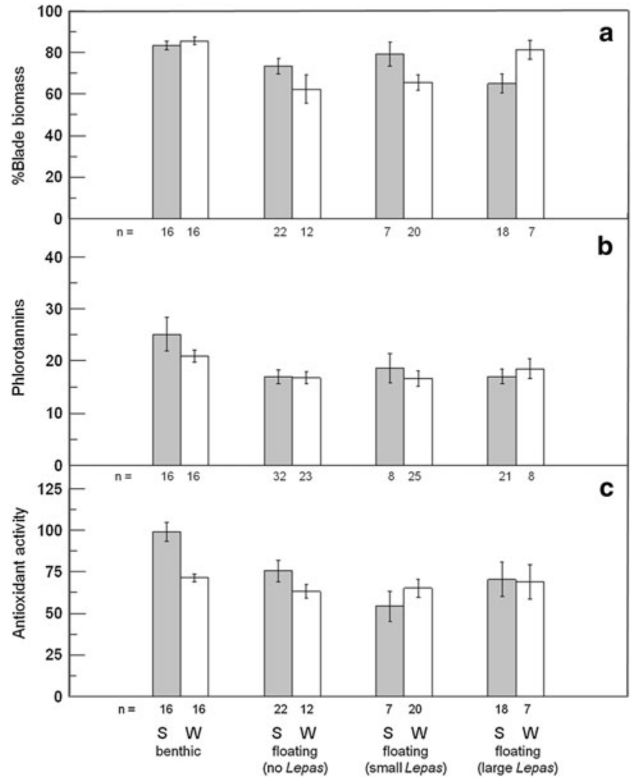

Fig. 2 **a** Percent of blade wet biomass by individual, **b** soluble phlorotannin contents (mg g^{-1} dw) and **c** antioxidant activity (µg TE g^{-1} ww) during summer (S) and winter (W) for benthic and floating *D. antarctica* without and with epibionts (*Lepas*). Figure shows mean ± SD, and the number below the bars represents *n* individuals considered; please note that for each algal category and season both study years were pooled

In general, the blade proportions of rafts were smaller than those of benthic algae in both Seasons (Fig. 2a). Significant differences in blade proportion were detected for Year, Algal status and the interaction between Season and Algal status (Table 2). The floating algae with small epibionts had a higher blade biomass in summer than in winter, but this pattern is reversed for algae with large epibionts (Fig. 2a). The blade proportions on rafts without epibionts and benthic kelps did not differ significantly between Seasons (Fig. 2a).

Physiological status of benthic and floating kelps

Phlorotannins and antioxidant activities

Benthic *D. antarctica* had higher levels of soluble phlorotannins than floating kelps, both in winter and in summer (Fig. 2b). There were significant differences for Year and Algal status and for the interactions Year–Season and Year–Algal status (Table 2). A clear seasonal difference in phlorotannin concentration (summer > winter) was only detected for the benthic population (Fig. 2b).

A similar general pattern as for phlorotannins was found for antioxidant activity, with a lower activity in floating compared to benthic algae (Fig. 2c). Also, benthic algae had higher antioxidant activity in summer than in winter. Significant effects were found only for the interaction between Year and Season (Table 2).

Table 2 Summary of MANOVA that found significant effects of the studied factors on response variables measured in benthic and floating *Durvillaea antarctica* from Coquimbo, northern Chile

Factors	Response variables	*P*
Year A	Percentage blade biomass	0.0068
	Phlorotannins	0.0296
Season B	Chlorophyll *a*	0.0022
	Maximal ETR	0.0001
	Maximal quantum yield (F_v/F_m)	0.0001
Algal status C	Percentage blade biomass	0.0004
	Phlorotannins	0.0005
	Maximal ETR	0.0167
A × B	Maximal ETR	0.0281
	Phlorotannins	0.0004
	Antioxidant activity	0.0213
A × C	Phlorotannins	0.0001
B × C	Percentage blade biomass	0.0047

Factors were Year (2010, 2011), Season (summer, winter) and the Algal status. 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 S3.)

Chlorophyll a

Pigment concentrations were significantly different only for the Season factor (Table 2). Higher values were found in winter than in summer for all algal categories (Fig. 3a). During the winter, the chlorophyll *a* concentrations in benthic *D. antarctica* tended to be slightly higher than in floating kelps, whereas in summer there were no differences between the four algal categories (Fig. 3a; Table 2 and S3).

Chlorophyll a fluorescence

Overall, floating *D. antarctica* had a similar photosynthetic efficiency as benthic algae, albeit with slight variations (Fig. 3b). The maximal quantum yield differed significantly only for Seasons (Table 2) with higher values in winter than in summer for all algal categories (Fig. 3b). Maximum ETR showed a similar pattern as maximal quantum yield, with lower values during the summer that also depended on Algal status (Fig. 3c). Significant differences were detected for Season, Algal status and the Year–Season interaction (Table 2).

Reproductive stages of benthic and floating bull kelp

Simplifying down from a saturated model (log-linear model and analysis of deviance), we detected that the interaction between Season and algal maturity was not significant for Algal status ($P = 0.4897$). However, a significant interaction occurred between algal maturity and Algal status ($P = 0.0270$) and between algal maturity and Season ($P = 0.0001$). The latter suggests a seasonal pattern in the occurrence of different maturity stages of *D. antarctica*, in which mature conceptacles (M) are mainly frequent during the winter and vegetative (V), immature (I) and senescent (S) are more common during the summer (Fig. 4). During the summer, the frequency of senescent samples was higher in the floating than in the benthic thalli (Fig. 4).

When the sex of the kelp samples was considered in the analyses, during the winter season the F_v/F_m values were similar for both sexes, with means of 0.65 ± 0.01 ($n = 28$) and 0.66 ± 0.01 ($n = 25$) for female and male kelps, respectively. However, during the summer the photosynthetic efficiency of female individuals was substantially lower (0.49 ± 0.02; $n = 10$) than that of males (0.60 ± 0.02; $n = 12$). Consequently, the photosynthetic efficiency (F_v/F_m) of *D. antarctica* depended significantly on sex, Season and the interaction between Season and sex (Table S5).

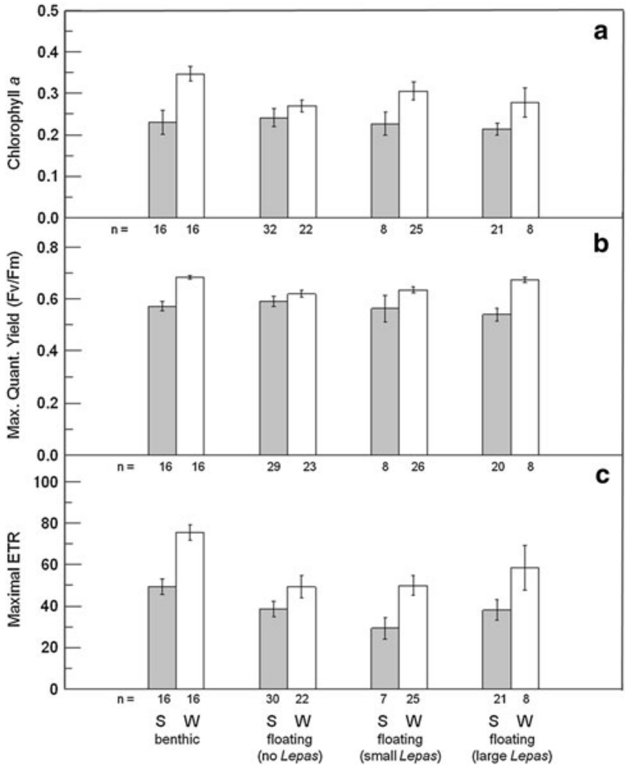

Fig. 3 Photosynthetic characteristic with respect to **a** chlorophyll *a* (mg g^{-1} ww), **b** maximal quantum yield (F_v/F_m) and **c** maximum electron transport rate (ETR_{max} μmol e− m^{-2} s^{-1}) during summer (S) and winter (W) for benthic and floating *D. antarctica* without and with epibionts (*Lepas*). Figure shows mean ± SD, and the number below the *bars* represents *n* individuals considered; please note that for each algal category and season both study years were pooled

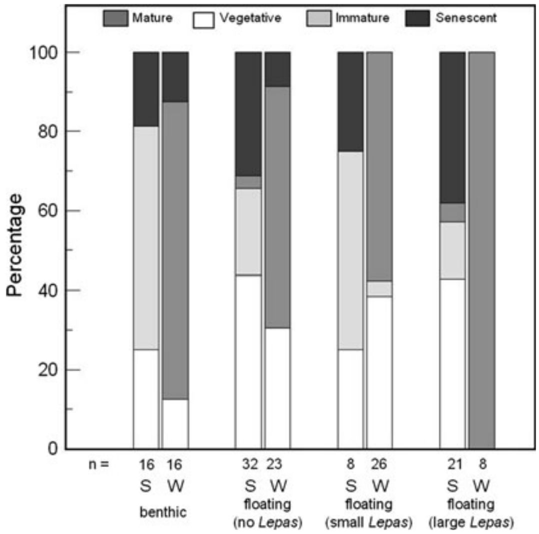

Fig. 4 Frequency of the four different reproductive stages (vegetative, immature, mature and senescent) of benthic and floating *D. antarctica* without and with epibiont (*Lepas*) during summer (S) and winter (W). Numbers indicate the number of algae per category of algal status; please note that for each algal category and season both study years were pooled

Discussion

Most rafts of *D. antarctica* found floating in the Coastal System of Coquimbo (CSC) were in relatively good conditions, with many of the measured parameters reaching similar values as the samples from the benthic population. However, Season (summer vs winter) and Algal status (based on *Lepas* presence and sizes) affected the morphological, physiological and reproductive parameters in different ways. The photosynthetic characteristics of benthic and floating algae depended primarily on Season, whereas blade biomass and phlorotannin concentrations were only affected by Algal status. Both factors together determine the floating capacity of *D. antarctica* at temperate latitudes (30°S) by directly influencing the acclimatization potential of algal rafts at the sea surface. The physiological health of floating *D. antarctica* appears to be compromised primarily during summer and after prolonged floating times.

Floating bull kelp in the study area

Based on growth estimates for *Lepas australis* (Skerman 1958) and the sizes of stalked barnacles on the bull kelp rafts sampled herein, rafts with different floating times were spread randomly throughout the study area without a clear spatial pattern. This distribution pattern can be explained by the fact that algae are occasionally caught in small gyres and also might be transported in southward directions while transiting through the study area. Oceanographic characteristics can facilitate the retention and convergence of floating objects in specific coastal zones (Kingsford 1995; Hinojosa et al. 2010). It is also possible that rafts with large *Lepas* have come from distant southern populations. The coastal oceanography in the study area is complex and highly variable, depending on the intensity and direction of coastal winds (Marín and Delgado 2007; Rahn et al. 2012; Aguirre et al. 2012), which likely influences the distribution and residence time of rafts within the CSC. This suggests that in our study area epibiont size is a better estimator of floating time than distance from source populations.

Floating seaweeds can be synergistically affected by abiotic and biotic factors that cause changes in growth and photosynthesis, similar as reported for benthic algae (Figueroa et al. 1997; Altamirano et al. 2000; Gómez et al. 2004, 2009). Herein, the smaller proportion of blade biomass in rafts was accompanied by lower values of phlorotannins and antioxidant activity, mainly caused by losses of the outer, photosynthetic layers of tissues. Experiments with tethered specimens of *D. antarctica* showed strong changes in biomass distribution and total length at the moment of sinking, with considerable reduction in blade biomass (>80 %) compared to stipes and holdfasts (Graiff et al. 2013). Furthermore, the effects of year on blade biomass and phlorotannin contents of floating and benthic kelps could have been caused by factors not examined herein. Interannual variations in population dynamics (recruitment, growth and mortality), different source populations of the sampled rafts, oceanographic conditions and higher/lower retention times in the CSC might have affected the algae differently in the two study years.

In general, the results suggest that after detachment floating *D. antarctica* acclimate to the conditions at the sea surface, as previously reported for the floating giant kelp *M. pyrifera* at ~30°S (Rothäusler et al. 2011d). *D. antarctica* inhabits the low intertidal zone, where it is exposed to sudden fluctuations of the physical environment by tidal and wave regimes (Westermeier et al. 1994; Hoffmann and Santelices 1997; Collantes et al. 2002). The dynamic photoacclimation capacity of *D. antarctica* is facilitated by its efficient photochemical adjustment to natural solar radiation (Cruces et al. 2012, 2013). The photochemical sensitivity to high temperatures could also help to understand the northern distribution limit of *D. antartica* near 30°S (Cruces et al. 2012, 2013). Therefore, *D. antarctica* rafts seem to be able to acclimate to new environmental conditions, but during summer and at lower latitudes (<30°S), the acclimation potential of this kelp appears to be limited.

Seasonal dynamics of benthic and floating algae

Seasonal patterns in light and temperature control growth, reproduction and physiological adjustment of seaweeds in temperate and polar regions (Lüning 1990; Davison 1991; Lüning and tom Dieck 1989; Wiencke et al. 2007). These processes, determined more exhaustively for benthic algae, are also expected to occur in similar ways in floating algae. Variable light conditions are the main driver of physiological acclimation and photosynthetic performance, often being accompanied by changes in concentrations of pigments and other molecules (Falkowski and LaRoche 1991; Rothäusler et al. 2011a). *Durvillaea antarctica* showed a more notable decrease in photosynthesis in response to Season (summer versus winter) than to Algal status (floating versus benthic). In experimental rafts of *M. pyrifera*, a decline in pigment contents has been observed within 15d of floating time (Rothäusler et al. 2011d). Those experiments had been conducted during the summer months, and despite the high light intensity at the sea surface, those rafts maintained high fluorescence values (Rothäusler et al. 2011d). *Durvillaea* rafts also were able to photoacclimate at the sea surface by lowering pigment concentrations and adjusting photosynthetic efficiencies, thereby extending the survival of detached kelps. Even during summer conditions, when environmental factors can be considered most stressful, photochemical potential to endure high solar radiation was observed in the benthic individuals. However, over prolonged floating periods, *D. antarctica* rafts accumulate costs and tissue losses (this study), which finally results in desintegration and sinking (Graiff et al. 2013).

Overall, the high photochemical potential enables algae with positive buoyancy to persist at the sea surface over short and midterm periods, but these responses can be costly during long-term persistence. Thus, other mechanisms, such as synthesis of phlorotannins and antioxidants, which operate in floating conditions in both seasons, can be involved in physiological acclimation. These substances support protective mechanisms against environmental stress (Mittler 2002; Gómez et al. 2009; Pansch et al. 2009). Rapid (within 2–6 h) induction of soluble phlorotannins stimulated by UV radiation has been described for *D. antarctica* as a short-term response to thermal stress, minimizing the effects of oxidative stress and maintaining photochemical processes (Cruces et al. 2012). However, photooxidized phlorotannins have been described from the peripheral tissues of *Hormosira banksii* thalli under high radiation (Schoenwaelder 2002). Although the production of phenolic compounds can be induced by solar radiation (Gómez and Huovinen 2010; Cruces et al. 2013), an increase in irradiation dosage during summer conditions can also provoke the exudation of phenols (Abdala-Díaz et al. 2006), which could be the reason for the lower values of phlorotannins in floating kelps. Loss of photosynthetic tissues during floating conditions could further limit the activation or maintenance of physiological protective mechanisms.

Water temperature also influences the growth and persistence of floating algae (Hobday 2000a; Vandendriessche et al. 2007; Rothäusler et al. 2009). Higher temperatures during summer enhanced the rates of tissue losses, which can lead to metabolic deficiencies (Brown et al. 1997; Cruces et al. 2013). Previous studies with *D. antarctica* showed that during summer, high water temperatures and intense solar radiation resulted in significant biomass losses and rapid tissue disintegration (Graiff et al. 2013). Consequently, experimental algae sank within less than 1 month during summer, whereas during moderate environmental conditions (cool water temperature and low solar radiation) prevailing in winter, spring and fall, floating *D. antarctica* persisted for >30 days at the sea surface (Graiff et al. 2013). Herein, we found rafts with large *Lepas* during both summer and winter, confirming that floating *D. antarctica* can survive in the study area for up to 30 days, regardless of the season. Seasonal variation in *Lepas* growth rates (e.g., Inatsuchi et al. 2010) needs to be considered for more precise estimates of floating times in future studies.

Reproductive characteristics of benthic and floating algae

The reproductive phenology of benthic and floating *D. antarctica* was in accordance with that described by Collantes et al. (2002). Mature individuals are usually found during winter in both benthic and floating conditions. The reproductive phenology in benthic populations of *D. antarctica* is poorly known along the Chilean coast, and local variations may be due to latitudinal or site-specific differences in environmental conditions (Santelices et al. 1980; Westermeier et al. 1994; Collantes et al. 2002), which might persist in floating rafts. Collantes et al. (2002) also observed reproductive activity in recently stranded individuals of *D. antarctica* in central Chile, but it was unknown where these had come from and how long they had floated at the sea surface. The higher frequency of senescent conceptacles (empty and with deteriorated tissues) in kelp rafts with large *Lepas* might indicate that floating time and environmental conditions during summer compromise their reproductive potential, as had previously been shown for *M. pyrifera* (Macaya et al. 2005; Hernández-Carmona et al. 2006; Rothäusler et al. 2011d). Detached thalli of *Hormosira banksii* also lost their reproductive potential more rapidly in summer than in autumn (McKenzie and Bellgrove 2008), supporting this suggestion. The capacity to generate and maintain reproductive products during floating trips determines the dispersal and colonization potential of a species (Macaya et al. 2005; Thiel and Gutow 2005b; Hernández-Carmona et al. 2006). The results of the present study confirm that floating *D. antarctica* have a high dispersal potential primarily during the winter months.

In seaweeds with separate sexes, physiological and ecological processes may differ between male and female individuals (Norton et al. 1985; Luxoro and Santelices 1989; Bulboa and Macchiavello 2001; Küster et al. 2005). Female plants of *D. antarctica* showed lower F_v/F_m in summer, which might be due to sex-specific responses in light acclimation as had been described for *Chara canescens* (Küster et al. 2005). Also, female reproductive investment with the formation of large reproductive cells (oosphere) might be much higher than in males (antherozoids). Moreover, differential allocation of photoprotectants between different reproductive structures could affect sex-specific tissue recovery during summer conditions (post-reproduction) and indirectly also the floating persistence of kelp rafts. Sexual variation in reproductive investment, physiological adjustment and floating persistence should be examined in future studies of *D. antarctica*, because it will affect the dispersal potential of this kelp.

Implications for rafting dispersal

Durvillaea rafts might have resided for extended time periods within the CSC as indicated by the raft distribution in relation to *Lepas* size. High densities of floating kelps are found off Pta. Lengua de Vaca, where the intense upwelling (e.g., Garreaud et al. 2011) might generate temporary fronts where floating algae (and other debris) commonly accumulate (Acha et al. 2004; Hinojosa et al. 2011). These oceanographic processes could thus suppress the dispersal potential of floating kelps.

The present study was conducted at the northern distribution limit of *D. antarctica* (Fraser et al. 2010b). The results confirm that kelp rafts have the potential to survive passage through the CSC, but that their dispersal capacity is reduced during the summer months. The seasonal variation in physiological/reproductive traits during floating conditions should also be considered from the climate change viewpoint, where increasing global temperatures and radiation levels may affect the dispersal potential and floating maintenance (Macreadie et al. 2011). Predictable changes in the atmospheric circulation for the Chilean coast in a scenario of warming climate could result in a modification of wind direction and intensification of coastal upwelling and circulation (Aiken et al. 2011). These changes will also affect the dispersal and persistence of floating algae.

Given the genetic differences between the clades of *D. antarctica* from central Chile and from the subantarctic region, and in particular the apparent differences in their dispersal potential (Fraser et al. 2009, 2010a, b), it appears timely to examine how the southern clade reacts to the conditions at the sea surface. Since environmental conditions (sea surface temperature and solar radiation) in the subantarctic region are more moderate than those at the northern distribution limit of this kelp, it can be hypothesized that in southern Chile floating *D. antarctica* survive much longer at the sea surface than observed herein. This hypothesis needs to be tested in future studies.

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