VI REDEALGAS WORKSHOP (RIO DE JANEIRO, BRAZIL)



Variation of the photosynthetic activity and pigment composition in two morphotypes of *Durvillaea antarctica* (Phaeophyceae) in the sub-Antarctic ecoregion of Magallanes, Chile

F. Méndez 1,2,3 1 · J. Marambio 1 · J. Ojeda 1 · S. Rosenfeld 1 · J. P. Rodríguez 1,2,3 · F. Tala 4,5 · A. Mansilla 1,2

Received: 26 March 2018 / Revised and accepted: 19 October 2018 / Published online: 9 November 2018 © Springer Nature B.V. 2018

Abstract

The environment of the sub-Antarctic ecoregion of Magallanes is highly heterogenous due to the influence of three oceans (Pacific, Atlantic, and Southern) and the effects of postglacial events such as the Last Glacial Maximum. In the sub-Antarctic ecoregion of Magallanes, the presence of two morphotypes of *Durvillaea antarctica* has recently been recorded that are related to the specific hydrodynamic configuration of the sites in the region. This study investigates the photosynthetic activity and pigment composition during two periods of the year in these two morphotypes of *D. antarctica*. One of them has broad and laminar fronds and occurs in wave-protected environments, while the other morphotype is characterized by cylindrical and elongated fronds and inhabits wave-exposed environments. The adult specimens of the "elongated-cylindrical" morphotype were collected in Seno Otway $(53.1^{\circ} \text{ S}, 71.5^{\circ} \text{ W})$ and the specimens of the "laminar" morphotype in Bahía el Águila, San Isidro $(53.7^{\circ} \text{ S}, 70.9^{\circ} \text{ W})$. ETR_{max}, α , and E_k as parameters of the ETR-E curves were higher for the "laminar" than the "elongated-cylindrical" morphotype, resulting in significant values. The concentration of fucoxanthin was statistically higher for the morphotype "laminar" compared to the morphotype "elongated-cylindrical." Both morphotypes exhibited different photosynthetic activities, perhaps attributed to their morphology, floatation capacity, and environment.

Keywords Durvillaea antarctica · Phaeophyceae · Morphology · Photosynthesis · Pigments · Sub-Antarctic · Ecophysiology

Introduction

The sub-Antarctic ecoregion of Magallanes is a very heterogeneous environment characterized by oceanographic

- F. Méndez fabiomendezmansilla@gmail.com
- Laboratorio de Macroalgas Antárticas y Subantárticas (LMAS), Facultad de Ciencias, Universidad de Magallanes, Casilla 113-D, Punta Arenas, Chile
- Instituto de Ecología y Biodiversidad (IEB), Las Palmeras 3425, 8320000 Santiago, Nuñoa, Chile
- Programa de Magister en Ciencias mención Manejo y Conservación de Recursos Naturales en Ambientes Subantárticos, Universidad de Magallanes, Casilla 113-D, Punta Arenas, Chile
- Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile
- Centro de Investigación y Desarrollo Tecnológico en Algas (CIDTA), Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile

gradients, different substrates, and seasonal variations in temperature, photoperiod, and irradiance (Dayton 1985; Silva and Calvete 2002). This stems from the presence of fjords, channels, postglacial lakes, and the shaping influence of postglacial events such as the Last Glacial Maximum (approximately between 23,000 and 19,000 years ago) (Fraser et al. 2009; Rosenfeld et al. 2015). The region's environmental heterogeneity has led to a benthic marine flora with a high degree of endemism and to species that are exposed to dynamic and continuous adaptive processes (Mansilla et al. 2013). As a consequence of global climate change, these processes have intensified (Rozzi et al. 2012).

The climate of the sub-Antarctic ecoregion of Magallanes is markedly different from the climate of cold and sub-Arctic temperate zones of the Northern Hemisphere (Rozzi et al. 2012). In the high latitudes of the Southern Hemisphere, the photoperiod and the intensity of solar radiation show significant seasonal changes that determine variations in the diversity and abundance of macroalgae (Ojeda et al. 2014). Solar radiation forms a gradient that decreases from the equator towards the poles and shows greater seasonal changes at high latitudes



than at low latitudes (Gunnarsson and Ingólfsonn 1995; Harley 2002; Tala et al. 2016). These latitudinal variations are important for species with wide distribution ranges and are important as triggers of biogeographic distribution patterns. These occur through the effects of temperature on physiological performances such as photosynthesis (Bischof et al. 2006a, b; Helmuth et al. 2006; Tala and Chow 2014).

Photosynthetic activity is directly related to the availability of light (Mansilla et al. 2016; Barinova 2017). Solar radiation strongly controls the zonation of macroalgae as it is crucial for their growth and distribution in benthic environments (Graiff et al. 2013; Tala et al. 2016). High irradiances of photosynthetically active radiation (PAR) and ultraviolet (UV) radiation can affect macroalgae (Kinzie 1993; Rautenberger et al. 2013; Fraser 2016). At high latitudes, solar radiation is a limiting factor, which is why the acclimatization strategies of macroalgae are fundamental in responding to this abiotic factor. They adapt their photosynthetic parameters (maximum electron transport rate, photosynthetic efficiency, and saturation irradiance) and their content/ratio of photosynthetic pigments (Tala and Chow 2014).

Among the macroalgae that dominate the exposed intertidal of the sub-Antarctic ecoregion of Magallanes, there are extensive populations of the species Durvillaea antarctica (Chamisso) Hariot, also commonly known in Chile as "cochayuyo" (Hay 1979; Fraser et al. 2010; Méndez et al. 2017). Durvillaea antarctica is a brown alga belonging to the Ochrophyta Division (Phaeophyceae), which lives in cold waters and is endemic to sub-Antarctic regions. This macroalgae has a circumpolar distribution in South America (Tierra del Fuego, Falkland Islands/Malvinas), southern Australia, Heard Islands, McDonald Islands, and New Zealand (Hoffmann and Santelices 1997; Fraser et al. 2009, 2012). In Chile, its distribution ranges from south of Coquimbo (29.9°S, 71.3° W) to the Diego Ramírez Islands (56.4° S, 68.7° W) (Santelices 1989; Ramírez and Santelices 1991; Cursach et al. 2014). The sub-Antarctic clade occurring in the Magallanes region is genetically very different from the clade of continental Chile (Fraser et al. 2010; Mansilla et al. 2017). Therefore, in accordance with these genetic differences, the existence of two different species should be considered (Mansilla et al. 2017). Durvillaea antarctica grows on rocky substrates in the low intertidal down to a depth of approximately 10 or 15 m is typical in areas highly exposed to waves (Mansilla et al. 2012) and occurs together with Lessonia spicata (formerly Lessonia nigrescens) (Mansilla et al. 2017).

Durvillaea antarctica is characterized by a dark greenishbrown color and can measure up to 15 m in length. They are fixed to the substrate by means of a conical disc compact with circular contour and smooth surface. From the disc, a distally flat, thick, and cylindrical stipe develops forming thick fronds of leathery consistency divided into many thin segments in the form of thick ribbons (blades) of different lengths that float on the surface of the sea (Hay 1979; Collantes et al. 2002). The blade of D. antarctica has a medulla that expands partially or completely into a structure similar to honeycomb. These numerous small vacuole-like spaces allow buoyancy as the main strategy against environmental factors such as waves (Stevens et al. 2002). This type corresponds to the species capable of floating which has been described for the Chilean coast. In the sub-Antarctic ecoregion of Magallanes a new morphotype of D. antarctica, which has not been sufficiently studied, has a short stipe, broad laminar fronds, and generally inhabits an environment protected from waves, has recently been reported and collected, which could constitute either a new species or a new ecotype of D. antarctica (Méndez et al. 2017). This new morphotype is identical to some species of the genus Durvillaea; without the ability of floating, it has been described that they have adapted to environments without wave exposure (South and Hay 1979; Cheshire et al. 1995; Fraser et al. 2009; Fraser et al. 2010; Fraser et al. 2012).

Knowledge about the ecophysiology of D. antarctica is crucial for several reasons: (1) It explains the evolutionary adaptation to different environments, taking into account the great environmental heterogeneity in Magallanes (Mansilla et al. 2016). (2) In the sub-Antarctic region, the high variability of PAR and UV radiation and the photoperiod considerably influences the abundance and biomass of macroalgae in the southernmost region. Therefore, it is important to understand the process of photosynthetic activity (photosynthesis and concentration of pigments) that allows macroalgae to acclimate to these environments (Bischof et al. 2006a,b; Marambio et al. 2016). (3) The genus Durvillaea is a marine resource that has been studied very little along the Chilean coast of Magallanes (Mansilla et al. 2017). Moreover, it has socioeconomic relevance at a national level and could generate new opportunities for small businesses and artisanal fishing based on its biological properties (anticoagulants, antitumor and antiviral), (Matsuhiro et al. 1996; Kelly and Brown 2000; Garrido and Parada 2008; Astorga-España et al. 2017); it is also a valuable nutritional source for direct human consumption (Astorga-España et al. 2017).

This study addresses the photosynthetic activity and composition of photosynthetic pigments in the two morphotypes of *D. antarctica*, with the aim of determining whether differences exist in the photosynthetic performance as well as the composition of main photosynthetic pigments and accessories in the morphotypes of *D. antarctica* that dwell in the two different localities in connection with the hydrodynamic factor in the two seasons of the year. This work contributes to the knowledge about algal diversity and their adjustment to the environment, as well as to the diversification of marine resources for the food, fishing, and biotechnological industries in the region of Magallanes and Chile.



Materials and methods

Description of localities of sampling

Seno Otway (53.1° S. 71.5° W). During October-November and in August, the surface seawater has a temperature of 8.9 °C and 5 °C, respectively. The salinity of the seawater surface amounts to 26.2 PSU and 25 PSU, respectively. The percentage of dissolved oxygen in the surface seawater is between 99.6% and 102% DO, respectively. These climate conditions are determined by the force of a wind system that is mainly in place in spring and summer. The habitat is exposed to the wind and waves that flow south-eastward (Valdenegro and Silva 2003; Martinic Beros 2002). In this wave-exposed locality, individuals of the morphotype EC (elongated cylindrical = EC) were collected (Fig. 1).

Bahía El Águila, near Cabo San Isidro (53.7° S, 70.9° W). In the course of October–November and August, the temperature of the surface seawater is 9.1 °C and 5.7 °C, respectively. The salinity of the surface seawater is 34.1 PSU and 32.4 PSU, respectively. The percentage of dissolved oxygen in the surface seawater is 142.4% DO and 97.7% DO, respectively. This environment has a near absence of a forceful wind system, as it is highly protected against the wind and waves that flow in a southeast direction (Valdenegro and Silva 2003). In this waveprotected locality, individuals of the morphotype L (laminar = L) were collected (Fig. 1).

75°0

54°S

75°0

Fig. 1 Sampling sites of the two morphotypes of Durvillaea antarctica in the sub-Antarctic waters of the Magellan ecoregion in southern Chile. Individuals of the morphotype with elongatedcylindrical blades (morphotype EC) were collected from Otway Sound (star-shaped, photo on the lower left). Individuals of the morphotype with laminar blades (morphotype L) occurred at Bahía El Aguila (circle-shaped, photo on the lower right) near Capo San Isidro in the Strait of Magellan

transportation. After this acclimation period, photosynthetic performance and composition of photosynthetic pigments were analyzed. Photosynthetic activity The photosynthetic performance of each frond of adult individuals (n = 7) of both morphotypes was measured using a 70°O ARGENTINA South Atlantic Morphotype EC

Sample collection

Individuals of *D. antarctica* (Ochrophyta, Phaeophyceae, Fucales) were collected in Seno Otway, a place exposed to the waves, and in Bahía El Águila near Cabo San Isidro, which is protected from the swell (Fig. 1). In order to achieve better representation of their respective localities, certain samplings were carried out during two seasonal periods: two samples collections between October and November of 2015 (austral spring), and two samples collections during August 2016 (winter). In terms of wind intensity, temperature, and irradiance these are contrasting seasons (Escobar et al. 1999-2008). Fronds were taken from seven adult individuals (n = 7) of each morphotype. These individuals were collected randomly through scuba diving in the upper intertidal (1-1.5 m depth). Subsequently, the individuals were transported in tanks filled with seawater to the Laboratorio de Macroalgas Antárticas y Subantárticas (LMAS) at the Universidad de Magallanes, Punta Arenas, Chile, where they were kept for 24 h in a temperature-controlled walk-in cabinet. Both temperature and photoperiod were adjusted according to the season. The acclimation to the laboratory conditions was carried out to allow the seaweeds to recuperate from stress during



Morphotype L

pulse-amplitude-modulated chlorophyll fluorometer "Diving-PAM" (Walz GmbH, Germany). The electron transport rate (ETR) was recorded at increasing intensities of actinic light (E = 0–3000 μ mol photons m⁻² s⁻¹) of the "Diving-PAM."

ETR values were estimated by multiplying the effective quantum yield of photosystem II (Φ PSII) with the corresponding intensity of the actinic light, as ETR = Φ PSII × E × A × 0.5; where E is the incident irradiance of actinic light, and A is the fraction of light absorbed from the thallus. The factor 0.5 assumes that electrons required to assimilate a CO₂ molecule are supplied by PSII (Huovinen and Gómez 2013). The absorption coefficient was measured by placing the fronds on a PAR sensor (PMA2200, USA), and calculating the light transmission (A = 1 – E_t / E_o), where E_o is the incident irradiance and E_t the irradiance transmitted under the algae fronds, according to methods indicated by Tala et al. (2013) and Huovinen and Gómez (2013).

ETRs were plotted against E, and the photosynthetic parameters were estimated by fitting these curves using the model of Jassby and Platt (1976): ETR_{max} × tanh (α × E/ETR_{max}), where ETR_{max} is the maximum ETR, tanh is the function of the hyperbolic tangent, α (an indicator of the efficiency of electron transport) is the initial slope of the P-E curve, and E is the incident irradiance. Finally, the saturation point of photosynthesis E_k was calculated as the ratio between ETR_{max} and α . The fitting of the curve was developed through the employment of the Kaleida Graph v4.0 program (Synergy Software, USA).

Composition of photosynthetic pigments

The modified method of Seely et al. (1972) was used for the extraction of chlorophyll a (Chl a), chlorophyll c (Chl c), and fucoxanthin (Fucox) from the fronds of seven individuals of both morphotypes (n = 7). Of the fronds, 0.125 g of fresh weight were taken, which were weighed with an analytical RADWAG balance (AS 220/C/2) and then semi-dried with absorbent paper to remove the seawater. Subsequently, 1 mL of dimetylsulfoxide (DMSO) was added to the weighted fresh biomass in a 50-mL tube. This was allowed to incubate for 15 min in complete darkness. Then, the supernatant was recovered and placed in a spectrophotometry cell to perform the analysis through a UV/visible spectrophotometer (Genesys 10 UV). Subsequently, the readings were performed at 480, 582, 631, and 665 nm wavelength. The quantification of photosynthetic pigments was carried out using the following equations (modification Seely et al. 1972):

Chl
$$a \text{ (mg g}^{-1}) = A_{665}/72.8$$

Chl $c \text{ (mg g}^{-1}) = (A_{631} + A_{582} - 0.297 \times A_{665})/61.8$
Fucox (mg g $^{-1}$) = $(A_{480} - 0.772 \times (A_{631} + A_{582} - 0.297 \times A_{665})/0.049 \times A_{665})/0.049 \times A_{665}/0.049 \times A_{665$



Data analysis

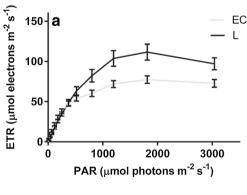
A generalized linear model (GLM) was handled with a quasi-Poisson distribution (appropriate for distribution cases, Zuur et al. 2009) aiming to study the factors and their significant resulting interactions. For the photosynthetic activity data (ETR_{max}, α , and E_k) and the composition of photosynthetic pigments (Chl c, Chl a, and Fucox), the factors considered were: morphotype and station. The statistical analysis was developed by using the R version 3.5.1 (R Development Core Team 2018).

Results

Photosynthetic activity

The ETR-E curves measured by PAM fluorometry in both morphotypes showed higher values for the L morphotype in austral spring (Fig. 2a) and higher values for morphotype EC in the winter season (Fig. 2b).

For the photosynthetic parameters (ETR_{max}, α , and E_k), the statistical analysis showed meaningful differences in the parameter ETR_{max} for morphotype EC between winter/austral spring (p = 0.000), in morphotypes EC and L between austral



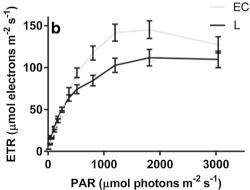


Fig. 2 Photosynthetic electron transport rate vs irradiance (ETR-E) curves of the two morphotypes (elongated-cylindrical, morphotype EC; laminar, morphotype L) of *D. antarctica*. Samplings of Austral spring (a) and of winter (b). Means and standard error are shown from seven measurements for each morphotype (n = 7)

spring/winter (p = 0.002), and between morphotypes EC and L during the austral spring (p = 0.004), (Fig. 3a,b). For α , differences statistically meaningful were not presented (Fig. 3c, d). Meanwhile, for E_k , there were meaningful differences exposed between the morphotypes EC and L during austral spring (p = 0.000) and the morphotype L between winter/austral spring (p = 0.000), see Fig. 3e, f.

By and large, higher values of ETR_{max} and E_k were shown for morphotype L in contrast with morphotype EC in the course of austral spring (Fig. 3a, e), while on the other hand, in winter the greater values of ETR_{max} and E_k were shown for the morphotype EC in comparison to morphotype L (Fig. 3b, f). The values of parameter α remained similar in austral spring (Fig. 3c) and in winter (Fig. 3d) in both morphotypes.

Composition of photosynthetic pigments

The extraction and quantification of photosynthetic pigments during the season of austral spring (Fig. 4a) and during the season of winter (Fig. 4b) did not show meaningful differences between the morphotypes (EC and L). Nevertheless,

Fig. 3 Photosynthetic parameters of the morphotypes "elongatedcylindrical" (EC) and "laminar" (L) of D. antarctica. Maximum electron transport rates (ETRmax, units: μ umol electrons m⁻² s⁻¹). electron transport efficiencies (initial slope of ETR-E curve or α units: µmol electrons $m^{-2} s^{-1} \mu mol photons m^{-2} s^{-1}$), and light saturation points of photosynthesis (E_k , units: μ mol photons m⁻² s⁻¹). Samplings of Austral spring (a, c, and e) and of winter (b, d, and f). Means and standard error are shown from seven measurements for each morphotype (n = 7). Asterisks indicate statistically significant differences between both morphotypes (P < 0.05)

higher values of Chl c and Fucox for the morphotype L, and higher values of Chl a for the morphotype EC during austral spring (Fig. 4a) were shown. Over winter, the values of the photosynthetic pigments were similar, being prominent the values of Fucox in both morphotypes, but being greater for the morphotype L (Fig. 4b). Respecting to the pigment relationships, the higher values of Fucox/Chl a in both seasons were notorious, highlighting the morphotype L with greater values in pigment relationships in both seasons differently from the morphotype EC (Fig. 4c, d).

Discussion

The present study shows significant ecophysiological differences between the morphotype laminar (L) and the morphotype elongated-cylindrical (EC) of the species *D. antarctica*. Both morphotypes were found in different places and exposed to various environmental conditions (Méndez et al. 2017). The seawater temperatures in Seno Otway and the Bahía El Águila near Cabo San Isidro are

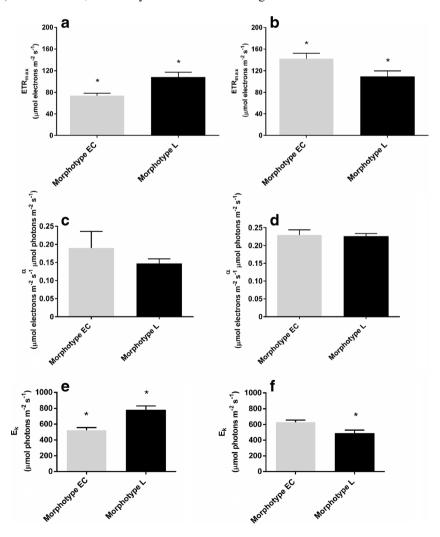
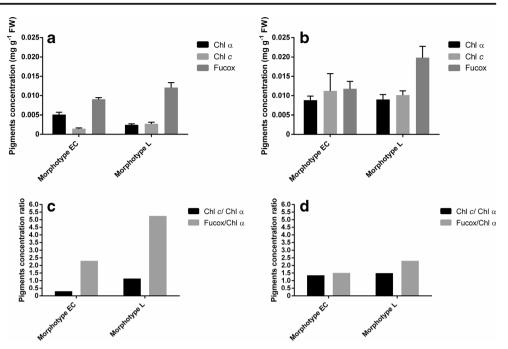




Fig. 4 Concentration of photosynthetic and major accessory pigments of the morphotypes "elongatedcylindrical" (EC) and "laminar" (L) of D. antarctica. Chlorophyll a (Chl a mg g⁻¹ FW), chlorophyll c (Chl c mg g⁻¹ FW), and fucoxanthin (Fucox mg g⁻¹ FW). Samplings of Austral spring (a) and of winter (b). Ratios of concentration of photosynthetic and major accessory pigments of the morphotypes "elongatedcylindrical" (EC) and "laminar" (L) of D. antarctica. Samplings of Austral spring (c) and of winter (d). Means and standard error are shown from seven measurements for each morphotype (n = 7)



similar all year round (ranging between ~ 4.5 °C in winter and 9.7 °C in summer), while salinity levels are generally lower in Seno Otway (28–30 PSU) than in the Bahía El Águila, near Cabo San Isidro (33–34 PSU), (Valdenegro and Silva 2003). One of the most notable differences between the two collection sites is their hydrodynamic environment. This factor can determine the morphology, physiology, ecology, and evolution of an organism in front of forces exerted by the waves (Venegas et al. 1993; Tala and Chow 2014; Tala et al. 2017). Organisms has anemones, hydrozoans, corals, or macroalgae tend to reorient and follow the flow, aiming to become more hydrodynamic, and transformed in similitude to the movement of the flow (Denny et al. 1998; Denny 1999). The continuous movements of the macroalgae produce an irregular and short-term variability of the availability of light on the surface of the thallus, generating lower dose and less damage produced by solar radiation (Tala et al. 2017). If D. antarctica manages to acquire a particular shape to resist wave flow (e.g., fronds elongated and cylindrical), it could obtain optimum photosynthetic performance for its survival, in terms of incident light energy (Denny 1999). Intertidal macroalgae that inhabit the continuous shores of Seno Otway, including D. antarctica (morphotype EC), are often exposed to strong waves as a consequence of the strong westerly winds in the Magallanes region. In contrast, the coast of the Strait of Magellan consists of numerous bays and small inlets where D. antarctica (morphotype L growing in Bahía El Águila, Cabo San Isidro) is protected from strong water movements and can grow in relatively calm waters (Méndez et al. 2017).

Other studies have presented identical patterns, such as morphological variations present in two morphotypes of *Durvillaea* in New Zealand. A morphotype with narrow fronds was observed in locations exposed to the environmental conditions, while another morphotype with wider fronds was found in relatively protected places. As a consequence, two species were identified, *Durvillaea willana* and *D. antarctica* (Cheshire and Hallam 1989; Cheshire et al. 1995; Fraser et al. 2009; Fraser et al. 2010). Similarly, *Durvillaea poha* was distinguished as a new species, posterior to morphological variations described in two morphotypes growing in parallel on the Australian coast (Fraser et al. 2012).

The results, in general, show that the morphotype L presents a higher physiological performance in agreement to the parameters ${\rm ETR}_{\rm max}$ and $E_{\rm k}$ differently from the morphotype EC during austral spring. Conversely, it is the subject observed in winter where the physiological performance is greater for the morphotype EC, according to the values that mirror the parameters ${\rm ETR}_{\rm max}$ and $E_{\rm k}$, at difference of the morphotype L. The pigment analysis showed similar values of Chl a and Chl c between both morphotypes and during the seasons; nonetheless, Fucox showed the higher values for the morphotype L in both seasons.

One of the important characteristics of the morphotype L is its wider and laminated fronds which could influence in the physiological performance. Leaf morphology could affect the light absorbance efficiency as shown by Mansilla et al. (2016) for species of the *Desmarestia* genus. As a consequence of the negative buoyancy of the morphotype L, it has several acclimation strategies to minimize irradiance fluctuation and thus maintain an optimal photosynthetic rate. Irradiance is a crucial factor for the photosynthetic rate (Colvard et al. 2014). This has been reflected in both the pigment content and the $E_{\rm k}$ parameter, the latter being an indicator of photoacclimation (Sakshaug et al. 1997). In this context, photoacclimation is a



physiological response to changes in irradiance that are either short term (seconds or minutes) or long term (days or months). At low irradiances, the macroalgae need to maximize the capture proficiency of light as well as its photosynthetic efficiency (Lüder et al. 2001; Koch et al. 2016; Sandbu 2017). It is probable that the morphotype L, which occurs at 1-1.5 m deep, and therefore, presents an irradiance of less saturation, increases the usage of photosynthetic pigments for capturing light. In this sense, the results of the austral spring showed contrasting values rather than macro algae that dwell with minor exposition to light; notwithstanding, the winter results harmonize with minor saturation irradiance, in agreement to the low degree of light exposition found in morphotype L. It is worth noting that the highest concentration of Fucox and the relationship Fucox/Chl a occurred in morphotype L in both seasons, probably owing to the laminate and wide fronds are found submerged at a higher depth without its fronds appearing in the surface, in comparison with the fronds of morphotype EC, which present permanent buoyancy. Morphotype L possesses zero buoyancy and, thereby, requires the operation of the complex filers pigment accessories to absorb energy in these environments with less degree of light exposition, adapting its photosynthetic system (numbers and sizes) at the disposition of light and nutrients, optimizing the photosynthesis. This also has been seen in other works (Lüder et al. 2001; Gómez et al. 2009).

The morphotype EC showed higher values with respect to the photosynthetic efficiency (α) and especially for Chl a. This is in accordance with the abovementioned results, since in this case, the morphotype shows a positive buoyancy favoring the occurrence of morphotype EC on the surface of seawater, similar to the rest of the populations of Durvillaea in continental Chile. This probably allows for a better and simpler capture of higher levels of irradiance and also the direct use of some of the main pigments like Chl a for photoacclimation (Gómez et al. 2009), as observed in the higher values of E_k in winter and of Chl a in austral spring and winter for the morphotype EC.

In agreement with Huovinen and Gomez (2011), the low values of $E_{\rm k}$, between 20–50 (µmol of photons m⁻² s⁻¹) and 14–16 m, tolerate the photosynthetic process. This also occurs in the Northern Hemisphere, which might generate a rank of "insecurity" in which the macroalgae can synthesize photosynthate in low-light conditions. This could explain how morphotype L, despite showing low values of $E_{\rm k}$, for instance in winter, and not possessing buoyance, has the capability of optimizing the photosynthesis process.

The hydrodynamics of the environment could also be considered a key factor for the acclimation of morphotype L, which is protected from the waves, and of morphotype EC, which is exposed to wave action. The seasonal oscillations change the light intensity of the different habitats in which the macroalgae grow, through the waves, affecting the optical characteristics of

seawater, generating turbidity, and as a consequence, influencing photosynthesis (Huovinen and Gomez 2011).

According to Colombo-Pallotta et al. (2006), water movement is essential for the morphology (stipes and/or fronds) of macroalgae. This has even led to the distinction of different species as in the case of the two kelp species from New Zealand fjords, *Ecklonia brevipes* (C. Agardh) J. Agardh and *Ecklonia radiata* (C. Agardh) J. Agardh. According to Colombo-Pallotta et al. (2006), macroalgae exposed to the waves have extended and thick fronds (resembling a belt) staying much longer on the surface of sea water, therefore, much more exposed to light energy. This suggests a more efficient light capture by these fronds. Meanwhile, the fronds that are wider and thinner and protected from the waves, probably do not have buoyancy, and would not receive considerable light energy, where acclimation strategies might take place, such as a greater concentration of accessory pigments as a complex antenna.

Several studies with macroalgae, such as the filamentous green alga Rhizoclonium, Fucus vesiculosus Linnaeus, Hypnea valentiae (Turner) Montagne, and Chondrus canaliculatus, show that salinity does not affect growth and maturation; however, low photosynthetic rates are observed when salinity levels are extremely low or high (0 or 45 PSU) of the salinity range in which the macroalgae are distributed (Edding et al. 2006; Mansilla et al. 2016). This shows a better growth and photosynthetic rate in intermediate salinities (30– 33 PSU) within the total range (Edding et al. 2006). This could contribute to a better photosynthetic performance in the area of Bahía El Águila, near Cabo San Isidro. Another factor, such as nutrients, is essential for the growth of macroalgae and is used according to the requirements of each species. For example, Desmarestia, which lives in Antarctic waters shows that a lack of nutrients can be crucial for its growth, decreasing its light capture (Edding et al. 2006; Mansilla et al. 2016). This would be interesting to evaluate in future studies, and see the implication of the two morphotypes with their respective nutrients.

Finally, there are numerous factors that regulate the ecophysiology of macroalgae, not only that of the morphotypes EC and L of *Durvillaea* that inhabit the different environmental conditions described, among them we highlight the following: (i) Solar radiation, as one of the main factors that regulate the concentration of pigments and the photosynthetic process (Colombo-Pallotta et al. 2006; Vanitha and Chandra 2012); (ii) light and photoperiod acclimation (Colombo-Pallotta et al. 2006; Marambio et al. 2016; Rautenberger et al. 2013); (iii) morphology of the thallus will probably determine the availability of light to be absorbed by the algae (Colombo-Pallotta et al. 2006; Mansilla et al. 2016; Méndez et al. 2017); and (iv) habitat of the species, its bathymetric distribution, and hydrodynamism. A clear example of adaptation to low irradiation and efficiency in light uptake is represented by Laminaria abyssalis Oliveira, compared to shallow water



912 J Appl Phycol (2019) 31:905–913

species such as *Laminaria digitata* Lamouroux (Colombo-Pallotta et al. 2006).

The present study is the first one to report the photosynthetic activity and pigment composition in two different morphotypes of the species *Durvillaea antarctica*. The two morphotypes differ in their form and photosynthetic activity, which is probably related to the distinct environmental conditions of their habitat. This could support the idea that the L morphotype is a new species. However, it is necessary to carry out genetic analyses to determine if there are different species of the *Durvillaea* genus in the region of Magallanes. This work could provide the basis for a later ecological, genetic, or speciation analysis, in addition to a probable new opportunity as a resource for the fishing and biotechnology industry both in the region of Magallanes and Chile.

Acknowledgments Project FONDECYT 1131023 to FT and AM (long-distance dispersal of macroalgae at high latitudes-floating kelp rafts capacity of nature under conditions along latitudinal), 1140940-AM (macroalgal adaptive radiation: potential links to the diversity of ecological niches in the Magellan and Antarctic ecoregion) and 1180433-AM (genomic, physiological, and ecological approaches to examine Antarctic and sub-Antarctic macroalgal responses to climate change and glacial retreat) of the National Council of Scientific and Technological Research of Chile (CONICYT). We are also grateful for the scholarships awarded by the Institute of Ecology and Biodiversity (IEB) to Fabio Méndez (ICM P05-002) and Juan Pablo Rodríguez (ICM P05-002). The facilities and equipment used for this study were kindly provided by the Laboratorio de Macroalgas Antárticas y Subantárticas (LMAS) and the Instituto de la Patagonia of the Universidad de Magallanes (UMAG) in Punta Arenas, Chile.

References

- Astorga-España MS, Mansilla A, Ojeda J, Marambio J, Rosenfeld S, Mendez F, Rodríguez JP, Ocaranza P (2017) Nutritional properties of dishes prepared with sub-Antarctic macroalgae - an opportunity for healthy eating. J Appl Phycol 29:2399–2406
- Barinova S (2017) Influence of macro-environmental climatic factors on distribution and productivity of freshwater algae. Int J Environ Sci Nat Res 4:1–5
- Bischof K, Gomez I, Molis M, Hanelt D, Karsten U, Lüder U, Roleda MY, Zacher K, Wiencke C (2006a) Ultraviolet radiation shapes seaweed communities. Rev Environ Sci Bio Technol 5:141–166
- Bischof K, Rautenberger R, Brey L, Perez-Llorens JL (2006b) Physiological acclimation to gradients of solar irradiance within mats of the filamentous green macroalga *Chaetomorpha linum* from southern Spain. Mar Ecol Prog Ser 306:165–175
- Cheshire AC, Hallam ND (1989) Morphological differences in the southern bullkelp (*Durvillaea potatorum*) throughout south eastern Australia. Bot Mar 32:191–197
- Cheshire AC, Conran JG, Hallam ND (1995) A cladistic analysis of the evolution and biogeography of *Durvillaea* (Phaeophyta) 1. J Phycol 31:644–655
- Collantes G, Merino A, Lagos V (2002) Fenología de la gametogénesis, madurez de conceptáculos, fertilidad y embriogénesis en *Durvillaea* antarctica (Chamisso) Hariot (Phaeophyta, Durvillaeales). Rev Biol Mar Oceanogr 37:83–112
- Colombo-Pallotta MF, García-Mendoza E, Ladah LB (2006) Photosynthetic performance, light absorption, and pigment

- composition of *Macrocystis pyrifera* (Laminariales, Phaeophyceae) blades from different depths. J Phycol 42:1225–1234
- Colvard NB, Carrington E, Helmuth B (2014) Temperature-dependent photosynthesis in the intertidal alga *Fucus gardneri* and sensitivity to ongoing climate change. J Exp Mar Biol Ecol 458:6–12
- Cursach JA, Suazo CG, Rau JR (2014) Depredación del lobo marino común *Otaria flavescens* sobre el pingüino de penacho amarillo *Eudyptes c. chrysocome* en Isla Gonzalo, Diego Ramírez, Sur de Chile. Rev Biol Mar Oceanogr 49:373–377
- Dayton P (1985) Ecology of kelp communities. Annu Rev Ecol Syst 16: 215–245
- Denny M (1999) Are there mechanical limits to size in wave-swept organisms?. J Exp Biol 202:3463–3467
- Denny M, Gaylord B, Helmuth B, Daniel T (1998) The menace of momentum: dynamic forces on flexible organisms. Limnol Oceanogr 43:955–968
- Edding M, Tala F, Vásquez J (2006) Fotosíntesis, productividad y algas marinas. Ediciones Universidad de La Serena, Chile, Filología vegetal
- Escobar I, Morales S, Undurraga A (1999–2008) Informe de Análisis de viento. Estaciones Meteorológicas. Armada de Chile. Centro Meteorológico Valparaíso. Chile
- Fraser CI (2016) Change in Southern Hemisphere intertidal communities through climate cycles: the role of dispersing algae. In: Hu Z, Fraser CI (eds) Seaweed Phylogeography. Springer, Dordrecht, pp 131–143
- Fraser CI, Nikula R, Spencer HG, Waters JM (2009) Kelp genes reveal effects of subantarctic sea ice during the Last Glacial Maximum. Proc Natl Acad Sci 106:3249–3253
- Fraser CI, Thiel M, Spencer HG, Waters JM (2010) Contemporary habitat discontinuity and historic glacial ice drive genetic divergence in Chilean kelp. BMC Evol Biol 10:203
- Fraser CI, Spencer HG, Waters JM (2012) *Durvillaea poha* sp. nov. (Fucales, Phaeophyceae): a buoyant southern bull-kelp species endemic to New Zealand. Phycologia 51:151–156
- Garrido DP, Parada RA (2008) Propiedades antioxidantes y funcionales de cinco algas chilenas sobre la calidad de pasta de salmón. Tesis
- Gómez I, Wulff A, Roleda MY, Huovinen P, Karsten U, Quartino ML, Dunton K, Wiencke C (2009) Light and temperature demands of marine benthic microalgae and seaweeds in polar regions. Bot Mar 52:593–608
- Graiff A, Karsten U, Meyer S, Pfender D, Tala F, Thiel M (2013) Seasonal variation in floating persistence of detached *Durvillaea* antarctica (Chamisso) Hariot thalli. Bot Mar 56:3–14
- Gunnarsson K, Ingólfsonn A (1995) Seasonal changes in the abundance of intertidal algae in southwestern Iceland. Bot Mar 38:69–77
- Harley CDG (2002) Light availability indirectly limits herbivore growth and abundance in a high rocky intertidal community during the winter. Limnol Oceanogr 47:1217–1222
- Hay CH (1979) Nomenclature and taxonomy within the genus *Durvillaea* Bory (Phaeophyceae: Durvilleales Petrov). Phycologia 18:191–202
- Helmuth B, Mieszkowska N, Moore P, Hawkins SJ (2006) Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. Annu Rev Ecol Evol Syst 37:373–404
- Hoffmann A, Santelices B (1997) Flora marina de Chile central. Edición Universidad Católica de Chile, Santiago de Chile
- Huovinen P, Gomez I (2011) Spectral attenuation of solar radiation in Patagonian fjord and coastal waters and implications for algal photobiology. Cont Shelf Res 31:254–259
- Huovinen P, Gómez I (2013) Photosynthetic characteristics and UV stress tolerance of Antarctic seaweeds along the depth gradient. Polar Biol 36:1319–1332
- Jassby AD, Platt T (1976) Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol Oceanogr 21:540–547



- Kelly BJ, Brown MT (2000) Variations in the alginate content and composition of *Durvillaea antarctica* and *D. willana* from southern New Zealand. J Appl Phycol 12:317–324
- Kinzie RA (1993) Effects of ambient levels of solar ultraviolet radiation on zooxanthellae and photosynthesis of the reef coral *Montipora* verrucosa. Mar Biol 116:319–327
- Koch K, Thiel M, Hagen W, Graeve M, Gómez I, Jofre D, Hofmann LC, Tala F, Bischof K (2016) Short- and long-term acclimation patterns of the giant kelp *Macrocystis pyrifera* (Laminariales, Phaeophyceae) along a depth gradient. J Phycol 52:260–273
- Lüder UH, Knoetzel J, Wiencke C (2001) Acclimation of photosynthesis and pigments to seasonally changing light conditions in the endemic Antarctic red macroalga *Palmaria decipiens*. Polar Biol 24:598–603
- Mansilla A, Ávila M, Yokoya NS (2012) Current knowledge on biotechnological interesting seaweeds from the Magellan region. Chile Rev Bras Farmacogn 22:760–767
- Mansilla A, Ávila M, Ramírez ME, Rodríguez JP, Rosenfeld S, Ojeda J, Marambio J (2013) Macroalgas marinas bentónicas de submareal somero de la ecoregión Subantártica de Magallanes, Chile. An Inst Patagon (Chile) 41:49–62
- Mansilla A, Méndez F, Murcia S, Rodríguez JP, Marambio J, Rosenfeld S, Yokoya N, Bischof K (2016) Adjustment of pigment composition in *Desmarestia* (Desmarestiaceae) species along a sub-Antarctic to Antarctic latitudinal gradient. Polar Res 35:29383
- Mansilla AO, Avila M, Cáceres J (2017) Reproductive biology of Durvillaea antarctica (Chamisso) Hariot in the sub-Antartic ecoregion of Magallanes (51–56° S). J Appl Phycol 29:2567–2574
- Marambio J, Mendez F, Ocaranza P, Rodriguez JP, Rosenfeld S, Ojeda J, Murcia S, Terrados J, Bischof K, Mansilla A (2016) Seasonal variations of the photosynthetic activity and pigment concentrations in different reproductive phases of *Gigartina skottsbergii* (Rhodophyta, Gigartinales) in the Magellan region, sub-Antarctic Chile. J Appl Phycol 29:721–729
- Martinic Beros M (2002) Breve historia de Magallanes. Ediciones de la Universidad de Magellanes, Punta Arenas 137 pp
- Matsuhiro B, Zuniga E, Jashes M, Guacucano M (1996) Sulfated polysaccharides from *Durvillaea antarctica*. Hydrobiologia 321:77–81
- Méndez F, Tala F, Rautenberger R, Ojeda J, Rosenfeld S, Rodríguez JP, Marambio J, Ocaranza P, Mansilla A (2017) Morphological and physiological differences between two morphotypes of *Durvillaea* antarctica (Phaeophyceae) from the sub-Antarctic ecoregion of Magallanes. Chile J Appl Phycol 29:2557–2565
- Ojeda J, Rosenfeld S, Marambio J, Rozzi R, Mansilla A (2014) Patrones estacionales y espaciales de la diversidad de moluscos intermareales de bahía Róbalo, canal Beagle, Reserva de la Biosfera Cabo de Hornos. Chile Rev Biol Mar Oceanogr 49:493–509
- Ramírez ME, Santelices B (1991) Catálogo de las algas marinas bentónicas de la Costa del Pacífico Temperado de Sudamérica. Monografías Biológicas 5. Pontificia Universidad Católica de Chile, Santiago de Chile
- Rautenberger R, Wiencke C, Bischof K (2013) Acclimation to UV radiation and antioxidative defence in the endemic Antarctic brown macroalga *Desmarestia anceps* along a depth gradient. Polar Biol 36:1779–1789
- R Development Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienne
- Rosenfeld S, Aldea C, Mansilla A, Marambio J, Ojeda J (2015) Richness, systematics, and distribution of molluscs associated with the

- macroalga *Gigartina skottsbergii* in the Strait of Magellan, Chile: a biogeographic affinity study. ZooKeys 519:49
- Rozzi R, Armesto JJ, Gutiérrez JR, Massardo F, Likens GE, Anderson CB, Poole A, Moses KP, Hargrove E, Mansilla AO, Kennedy JH, Willson M, Jax K, Jones CG, Callicott JB, Kennedy JH (2012) Integrating ecology and environmental ethics: earth stewardship in the southern end of the Americas. BioScience 62:226–236
- Sakshaug E, Bricaud A, Dandonneau Y, Falkowski PG, Kiefer DA, Legendre L, Morel A, Parslow J, Takahashi M (1997) Parameters of photosynthesis: definitions, theory and interpretation of results. J Plankton Res 19:1637–1670
- Sandbu M (2017) High arctic sea-ice algae-the use of rapid light curves to assess photosynthetic performance of different ice-algal communities. Master's thesis, Norwegian University of Science and Technology
- Santelices B (1989) Algas marinas de Chile. Distribución. Ecología. Utilización. Diversidad. Ediciones Universidad Católica de Chile, Santiago
- Seely GR, Duncan MJ, Vidaver WE (1972) Preparative and analytical extraction of pigments from brown algae with dimethyl sulfoxide. Mar Biol 12:184–188
- Silva N, Calvete C (2002) Características oceanográficas físicas y químicas de canales australes chilenos entre el golfo de Penas y el estrecho de Magallanes. CIMAR 2 Fiordos. Cienc Tecnol Mar 25: 23–88
- South GR, Hay CH (1979) Influence of wave action and latitude on morphology and standing crop of New Zealand *Durvillaea* antarctica (Chamisso) Hariot (Phaeophyta, Durvilleales). J Roy Soc NZ 9:289–296
- Stevens CL, Hurd CL, Smith MJ (2002) Field measurement of the dynamics of the bull kelp *Durvillaea antarctica* (Chamisso) Hariot. J Exp Mar Biol Ecol 269:147–171
- Tala F, Chow F (2014) Ecophysiological characteristics of *Porphyra* spp. (Bangiophyceae, Rhodophyta): seasonal and latitudinal variations in northern-Central Chile. J Appl Phycol 26:2159–2171
- 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). Mar Biol 160:1339–1351
- Tala F, Velásquez M, Mansilla A, Macaya EC, Thiel M (2016) Latitudinal and seasonal effects on short-term acclimation of floating kelp species from the south-East Pacific. J Exp Mar Biol Ecol 483:31–41
- Tala F, Penna-Díaz MA, Luna-Jorquera G, Rothäusler E, Thiel M (2017) Daily and seasonal changes of photobiological responses in floating bull kelp *Durvillaea antarctica* (Chamisso) Hariot (Fucales: Phaeophyceae). Phycologia 56:271–283
- Valdenegro A, Silva N (2003) Caracterización oceanográfica física y química de la zona de canales y fiordos australes de Chile entre el estrecho de Magallanes y cabo de Hornos (CIMAR 3 Fiordos). Ciencia y Tecnología del Mar 26:19–60
- Vanitha A, Chandra S (2012) Studies on photosynthetic pigments of some red algae of Covelong, Chennai (India). Int J Curr Res 149–154
- Venegas M, Matsuhiro B, Edding ME (1993) Alginate composition of Lessonia trabeculata (Phaeophyta: Laminariales) growing in exposed and sheltered habitats. Bot Mar 36:47–52
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) GLM and GAM for count data In: Mixed effects models and extensions in ecology with R. Springer, New York, NY, pp. 209–243

