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Bio-optical and physiological patterns in Antarctic seaweeds: A functional trait based approach to characterize vertical zonation

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ABSTRACT

A suite of photosynthetic and bio-optical properties of 29 Antarctic seaweeds from Fildes Bay, King George Island, were studied in order to address the question whether their different functional traits, grouped according to gross morphology, bathymetric distribution, taxonomic category and biogeographic affinity, can explain the observed patterns of vertical distribution and relevant ecosystems services. Based on PCA analysis light requirements for photosynthesis (E_k), thallus absorbance and thickness, photosynthetic efficiency (α) and tolerance to stress (UV and temperature) were the traits with the highest predictive value for vertical distribution of the studied Antarctic algae. In this context, the set of bio-optical traits were strongly related with a morphological adaptation to use the available light at different wavelengths at different depths: thick leathery and coarsely branched morphs, mostly red and brown algae, were well equipped to absorb the impoverished light field at deeper locations (lowest E_k values close to $36 \mu\text{mol m}^{-2} \text{s}^{-1}$), while sheet-like algae, especially green algae showed lower absorption at wavelengths that are rapidly attenuated with depth (highest E_k values of $260 \mu\text{mol m}^{-2} \text{s}^{-1}$). The studied algae showed high tolerance to stress measured in short-term exposures to UV radiation and enhanced temperature (7°C). The stress tolerance was independent of gross morphology, while greatest differences were found along depth gradient and between algae of different biogeographic affinity. The studied traits were highly interlinked in terms of photosynthetic and bio-optical properties. Our trait based framework defined three major clusters of species: (1) delicate (filamentous and sheet-like) green algae, living mostly in the intertidal zone and with wide geographic distribution; (2) thick leathery Rhodophyta with Antarctic-Subantarctic origin, found mostly at shallow-subtidal locations; and (3) endemic Antarctic brown algae with thick morphology inhabiting the lower subtidal zone. Overall, these results highlight the importance of morpho-functional traits of macroalgae in explaining their distribution across a depth gradient and provide insights into their potential to endure a changing polar environment. This is relevant in Antarctic marine ecology as macroalgae underpin the biogeochemical processes at coastal ecosystems.

1. Introduction

Marine macroalgae are vertically zoned and along the depth gradient these organisms experience different sets of environmental conditions. Due to such differences, macroalgae inhabiting different depth levels are expected to display different fitness and physiological performance in response to ambient environmental conditions. Recently, trait approach has been widely used to assess the distribution of functional entities that can be scaled up to community structure and ecosystem functioning along different environmental gradients (Grime, 1981; Lavorel and Garnier, 2002; Ackerly and Cornwell, 2007). This concept, known in ecology as “the holy grail framework”, has been

revitalized in the last decades in the context of the contemporary climate change (Chapin, 2003; Suding et al., 2008; Kominoski et al., 2013)

In the case of marine communities dominated by macroalgae, the classic functional-form models proposed by Littler and Littler (1980) or Steneck and Watling (1982) pointed to link gross morphology, physiological performance and physical gradients assuming that macroalgal species with similar or at least comparable gross morphology share also similar ecophysiological features, i.e. the models set predictions of functional properties based on an examination of forms. For example, algae attaining sheet-like morphology are predicted to have higher growth rates, photosynthesis and nutrient uptake, lower resistance to herbivory and lower competitive capacity than algae with

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more robust morphologies (reviewed by Hurd et al. (2014)). Due to their conceptual functionality, macrophyte trait-based approaches have also been used to detect changes in the ecosystem condition (Orfanidis et al., 2003; Engelhardt, 2016; Balata et al., 2011), distributional patterns (Gaspar et al., 2017) or to evaluate shifts of functional diversity in scenarios of global climate change (Strain et al., 2014).

Studies revisiting the relationship between form-function and depth distribution of macroalgae from different geographical regions have also reported contrasting results, reinforcing the idea that there is not a uniform scheme of zonation, but that this varies locally depending on the species composition and physical and biological processes operating at each site (Ingólfsson, 2005). On the other hand, macroalgae can show a variety of morphologies within one life history and even during their ontogeny (Hurd et al., 2014). However, practically all studies appear to coincide that gradients in irradiance define the ordination of aquatic macrophytes along the shore, and thus, their morpho-functional attributes (Markager, 1993; Enríquez et al., 1994; Gómez et al., 2004). For example, in macroalgal assemblages from the Swedish and south Chilean coast, a clear dependence of photosynthetic characteristics on gross morphology along the depth profile was demonstrated (Johansson and Snoeijs, 2002; Gómez and Huovinen, 2011). However, a morphology based form-function concept could not explain the observed physiological and ecological patterns displayed by macroalgae in the context of stress tolerance, especially in those intertidal assemblages periodically submitted to extreme temperatures, salinity, desiccation, solar radiation, etc. (Gómez and Huovinen, 2011; Cruces et al., 2012). For example, various metabolic adaptations developed to cope with enhanced solar radiation, e.g. photochemical down-regulation via photoinhibition, are strongly dependent on the position on the shore, but not on gross morphology (Aguilera et al., 1999). This can have important consequences for primary productivity as the life strategy is a trade-off between life/morphology related traits and environmental tolerance characteristics (Jänes et al., 2016).

Antarctic macroalgae show, not only shade adapted photosynthetic characteristics (revised in Gómez et al., 2009), but also are metabolically well equipped to cope with environmental stress (e.g. temperature changes and UV radiation) (Rautenberger et al., 2013; Huovinen and Gómez, 2013). For example, UV tolerance mechanisms can operate in deeper algae, which are not normally exposed to UV radiation (Gómez and Huovinen, 2015). Thus, it is essential to evaluate whether distinct coexisting species sharing similar functional traits categorized in gross morphology, taxonomic or biogeographical affinity show comparable photosynthetic and bio-optical properties in the Antarctic environment in order to estimate the ecological significance of functional diversity in the community assembly (Díaz and Cabido, 2001; Marks and Lechowicz, 2006). In fact, the abundance and species diversity has been associated with the prevalence of some dominant traits that finally determine different properties of the community such as stability, niche partitioning, facilitative interactions etc. (Westoby and Wright, 2006). These features are strongly challenged when the community is subjected to multiple perturbations (Mouillot et al., 2013). In littoral systems exposed to strong perturbation by ice, species richness and hence, functional diversity is an important factor that allow the benthic community withstanding physical stress (Scrosati and Heaven, 2007). In King George Island, Antarctica, structure of the benthic ecosystem is strongly determined by the species diversity, while the mesoscale biomass patterns were accounted mainly by the abundance of algal taxa with key functional traits, e.g. canopy-forming algae with leathery and coarsely branched morphology (Valdivia et al., 2015). In scenarios of regional climate change in the Antarctic marine realm, the diversity and distribution of macroalgal traits that confer tolerance to a broad spectrum of environmental conditions likely become dominant within future communities (Harley et al., 2012).

In the present study we examine whether the photosynthetic (P-I based parameters, tolerance to stress) and bio-optical traits (thallus thickness, area/weight ratio and absorbance) of Antarctic macroalgae

can be associated with their gross morphology, bathymetrical distribution, biogeographic affinity, and taxonomic status. A multivariate ordination technique was used to simplify relationships between the different functional traits and define photosynthetic, bio-optical and tolerance trait clusters in a macroalgal assemblage. For example, traits conferring enhanced light absorption (e.g. thicker thallus and high absorbance) could be favored in subtidal zones, while traits developed to withstand extreme changes in physical environment (e.g. small size, rapid metabolic adjustments, large area/weight ratio) would be advantageous at intertidal locations (Gómez and Huovinen, 2010). In this context, the present study is a first effort in order to put physiological information from Antarctic macroalgae into an ecological perspective and to gain insights into the functional traits that shape the structure of these communities subjected to extreme physical constraints at different spatial and temporal scales.

2. Materials and methods

2.1. Macroalgal assemblages

The zonation pattern of Antarctic seaweeds is marked by the arrangement of species with different size and morpho-functional characteristics (Fig. 1). The intertidal rocky shores are dominated by turf species, mainly small filamentous Chlorophyceans < 20 cm in length. In contrast, in subtidal zone between 5 and 40 m, an exuberant vegetation of canopy-forming species, such as large perennial Desmarestiales (*Desmarestia anceps*, *D. menziesii* and *Himantothallus grandifolius*) can be recognized. These algae normally display a thick leathery or coarsely branched morphology. Delicate species of Rhodophyta such as *Pantoneura plocamioides* and *Myriogramme smithii* can be found at deep locations normally as understory assemblages. Similar as the large endemic brown algae, red algae with coarsely branched form and thallus lengths between 30 and 100 cm, e.g. the pseudoperennial *Palmaria decipiens* and *Iridaea cordata*, show a wide vertical distribution, growing from 20 m in the subtidal to intertidal locations (in Fig. 2 some representative species of these functional groups are shown). The arrangement is strongly determined by physical factors, especially by light availability in the subtidal zone below 5 m, the seasonal perturbation caused by ice scouring that govern the algal colonization in the upper subtidal zone between 0 and 5 m, whereas at the intertidal zone, the marked impact of ice, snow, extreme changes of UV radiation and temperature restrict the presence of macroalgae to intertidal pools and rocky crevices (Gambi et al., 1994; Klöser et al., 1994; Smale, 2008; Huovinen and Gómez, 2013).

2.2. Determination of underwater solar radiation

Profiles of spectral solar irradiation were measured with a hyperspectral radiometer RAMSES-ACC2-UV-vis (Trios Optical Sensors, Oldenburg, Germany). Around noon (12:00–14:00 h), the device was submerged at intervals of 1 m down to a 16 m depth with a minimum of three measurements per depth. Values of Photosynthetically Active Radiation (PAR, 400–700 nm), UV-A (315–400 nm) and UV-B (300–315 nm) were used to determine the attenuation coefficient (K_d) according to equation $E_d(z) = E_d(0) e^{-K_d z}$, where K_d is the vertical diffuse attenuation coefficient for downward irradiance, $E_d(z)$ the downwelling irradiance at depth z , and $E_d(0)$ the irradiance right below the surface (Kirk, 2011). K_d values were calculated from the slope of the linear regression of the natural logarithm of irradiance vs. depth for each wavelength. Average K_d were 0.55, 0.28 and 0.15 m^{-1} for UV-B, UV-A and PAR wavelength bands, respectively. These values corresponded to coastal water type 3 according to Jerlov's (1976) classification.

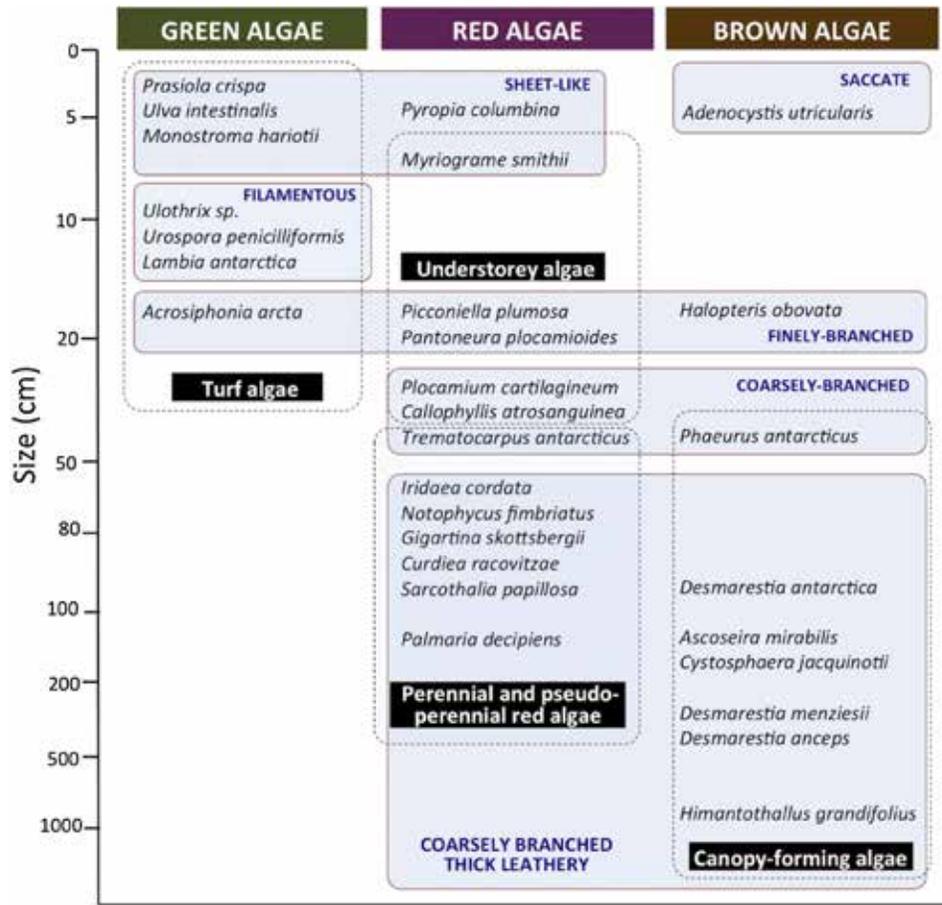


Fig. 1. List of studied Antarctic macroalgae according to their morpho-functional characteristics and ecological functions (sensu Littler and Littler, 1980; Steneck and Dethier, 1994).

2.3. Determination of photosynthetic and bio-optical traits

The most conspicuous seaweed species of red (13), brown (9) and green algae (7) were collected at Fildes Bay, King George Island (62°12'S) during the summer season (Fig. 1). The algae were transported in seawater filled containers to the laboratory at the Antarctic

station ‘Base Profesor Julio Escudero’, where they were carefully cleaned and washed with filtered (0.45 µm) seawater. In the case of large brown and red algae (e.g. *Desmarestia*, *Himantothallus* or *Palmaria*) thallus pieces from the apical zone of (20 cm in length) were used. Prior to experimentation, the algal material was incubated separately in 1-L plastic vessels with filtered seawater at 2 ± 1 °C with aeration for at

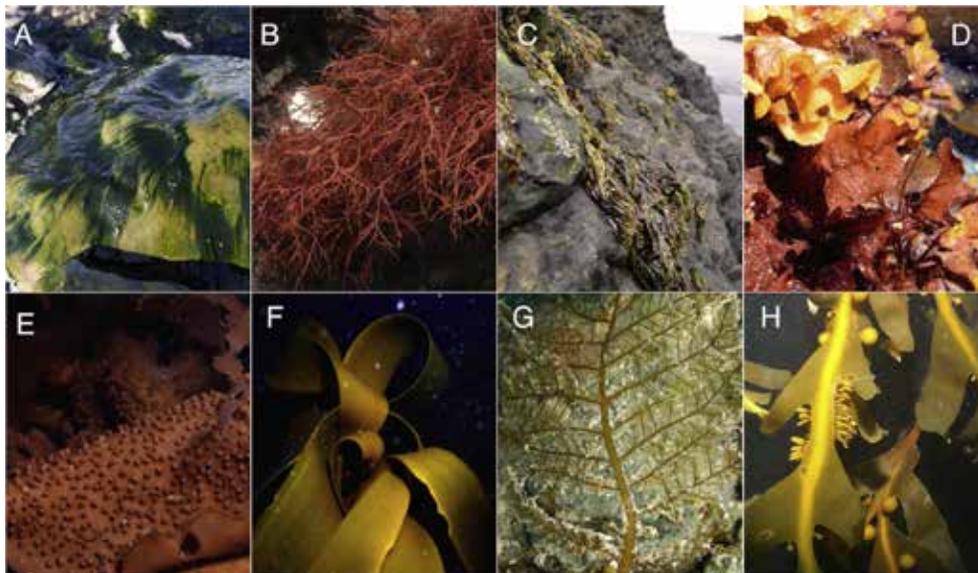


Fig. 2. Antarctic macroalgae and examples of morphologies used in the functional trait matrix. (A) *Urospora penicilliformis* (turf, filamentous); (B) *Pantoneura plocamioides* (understorey, finely branched); (C) *Pyropia endiviifolia* (turf, sheet-like); (D) *Phycodris* sp. (understorey, sheet-like); (E) *Gigartina skottsbergii* (perennial red alga, thick leathery); (F) *Ascoseira mirabilis* (canopy-forming, thick leathery); (G) Young exemplar of *Desmarestia* sp. (canopy-forming, coarsely branched); (H) *Cystosphaera jacquinotii* (canopy-forming, thick leathery). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

List of studied macroalgae and their physiological and bio-optical traits used for analyses. Values for original data are means \pm D.S. Units: Alpha ($\mu\text{mol e}^{-}\text{m}^{-2}\text{s}^{-1}$)($\text{m}^{-2}\text{s}^{-1}$) $^{-1}$; E_k ($\text{m}^{-2}\text{s}^{-1}$); ETR ($\mu\text{mol e}^{-}\text{m}^{-2}\text{s}^{-1}$); Absorbance (rel units); Thickness (mm); Stress index (% control of tolerance to UV/T°). Intertidal (int); Shallow subtidal(ss); deep subtidal (dp). In parenthesis are denoted the species abbreviations used through the text and figures.

	Alpha	E_k	ETR _{max}	Absorbance	Thickness	Area/weight ratio	Stress index
Red algae							
<i>Pyropia endiviifolia</i> (Pyend)	0.11 \pm 0.02	96.61 26.13	10.82 \pm 1.76	0.69 \pm 0.12	59.74 \pm 2.55	100.61 \pm 11.69	85.17 \pm 3.46
<i>Iridaea cordata</i> (int) (Ircor-i)	0.18 \pm 0.04	101.76 \pm 15.17	18.61 \pm 2.08	0.79 \pm 0.04	410.50 \pm 56.92	37.43 \pm 6.64	118.36 \pm 4.00
<i>Palmaria decipiens</i> (Padece)	0.17 \pm 0.05	78.58 \pm 17.66	13.36 \pm 3.97	0.66 \pm 0.11	347.42 \pm 33.56	18.76 \pm 2.46	92.13 \pm 4.57
<i>Pantoneura plocamioides</i> (Panplo)	0.13 \pm 0.01	149.39 \pm 30.06	19.47 \pm 3.62	0.81 \pm 0.01	598.75 \pm 85.02	56.85 \pm 8.23	
<i>Iridaea cordata</i> (ss) (Ircor-ss)	0.14 \pm 0.02	121.26 \pm 27.53	17.26 \pm 5.33	0.80 \pm 0.05	584.75 \pm 51.59	34.63 \pm 16.05	108.53 \pm 1.13
<i>Gigartina skottsbergii</i> (Giskott)	0.18 \pm 0.06	69.19 \pm 3.46	12.93 \pm 5.01	0.89 \pm 0.02	678.25 \pm 13.07	8.59 \pm 2.46	78.65 \pm 2.82
<i>Myriogramme smithii</i> (Mysmi)	0.17 \pm 0.10	52.17 \pm 14.12	9.24 \pm 6.83	0.74 \pm 0.06	590 \pm 146.36	11.70 \pm 5.48	
<i>Plocamium cartilagineum</i> (ss) (Plocar-ss)	0.12 \pm 0.01	103.64 \pm 5.76	12.57 \pm 0.61	0.71 \pm 0.02	327.66 \pm 3.05		87.01 \pm 1.22
<i>Sarcothalia papillosa</i> (Sarpa)	0.12 \pm 0.05	46.51 \pm 33.99	4.83 \pm 1.55	0.76 \pm 0.02	699.75 \pm 22.42	14.81 \pm 0.90	
<i>Curdiea racovitzae</i> (ss)(Curdrac-ss)	0.07 \pm 0.01	92.73 \pm 8.22	7.04 \pm 0.19	0.87 \pm 0.06	482 \pm 19.98	15.33 \pm 1.08	39.60 \pm 21.44
<i>Trematocarpus antarcticus</i> (Treat)	0.13 \pm 0.05	46.53 \pm 33.15	5.13 \pm 1.84	0.80 \pm 0.01	323 \pm 16.75	21.44 \pm 0.37	
<i>Plocamium cartilagineum</i> (ds) (Plocar-ds)	0.06 \pm 0.03	140.23 \pm 59.24	9.47 \pm 7.97	0.81 \pm 0.04	280.12 \pm 39.19	34.99 \pm 8.08	52.08 \pm 13.69
<i>Callophyllis</i> sp. (Calloph)	0.19 \pm 0.04	117.99 \pm 26.24	21.96 \pm 3.72	0.75 \pm 0.02	340.25 \pm 10.27	80.13 \pm 6.46	60.75 \pm 11.26
<i>Notophycus fimbriatus</i> (Nothop)	0.15 \pm 0.03	81.97 \pm 33.73	11.70 \pm 2.78	0.81 \pm 0.01	671.25 \pm 18.41	13.81 \pm 1.39	71.58 \pm 4.49
<i>Picconella plumosa</i> (Picplu)	0.13 \pm 0.02	45.16 \pm 15.14	5.94 \pm 1.34	0.76 \pm 0.05	194.75 \pm 74.72	173.58 \pm 15.79	
<i>Curdiea racovitzae</i> (Curdrac-ds)	0.06 \pm 0.04	168.50 \pm 109.1	7.80 \pm 4.30	0.80 \pm 0.02	482 \pm 19.07	15.54 \pm 1.22	
Brown algae							
<i>Adenocystis utricularis</i> (Adeutr)	0.21 \pm 0.02	136.52 \pm 36.21	29.31 \pm 6.84	0.85 \pm 0.02	139.25 \pm 5.14	13.75 \pm 1.66	89.37 \pm 3.66
<i>Desmarestia antarctica</i> (Desant)	0.14 \pm 0.01	165.30 \pm 74.74	22.51 \pm 9.07	0.67 \pm 0.03	262.25 \pm 41.37	25.09 \pm 3.89	80.89 \pm 7.59
<i>Desmarestia anceps</i> (Desanc)	0.13 \pm 0.03	121.26 \pm 32.40	16.56 \pm 7.08	0.81 \pm 0.04	438.18 \pm 31.63	41.80 \pm 1.78	88.27 \pm 2.59
<i>Himantothallus grandifolius</i> (Himgra)	0.20 \pm 0.04	68.31 \pm 27.26	13.06 \pm 3.72	0.88 \pm 0.03	912 \pm 74.37	10.77 \pm 0.67	93.22 \pm 2.16
<i>Ascoseira mirabilis</i> (Ascmir)	0.22 \pm 0.02	78.35 \pm 29.22	17.24 \pm 5.06	0.79 \pm 0.02	571.75 \pm 159.13	20.87 \pm 3.02	91.26 \pm 2.25
<i>Cystosphaera jacquinotii</i> (Cisjacq)	0.20 \pm 0.03	36.12 \pm 8.68	7.25 \pm 2.06	0.73 \pm 0.01	2166.66 \pm 269.66	24.68 \pm 3.28	77.16 \pm 4.16
<i>Desmarestia menziesii</i> (Desmen)	0.24 \pm 0.09	56.12 \pm 26.06	12.46 \pm 3.27	0.93 \pm 0.04	1137.33 \pm 103.36		87.87 \pm 4.55
<i>Phaeurus antarcticus</i> (Phaeant)	0.15 \pm 0.02	111.78 \pm 16.14	16.99 \pm 1.52	0.93 \pm 0.03	899.2 \pm 84.06		90.78 \pm 3.45
Green algae							
<i>Acrosiphonia arcta</i> (Acroarct)	0.18 \pm 0.01	192.18 \pm 33.00	34.51 \pm 6.77	0.66 \pm 0.05	102.83 \pm 2.06	58.33 \pm 14.12	87.12 \pm 4.60
<i>Monostroma hariotii</i> (Monha)	0.20 \pm 0.05	53.94 \pm 7.18	10.88 \pm 1.74	0.49 \pm 0.11	24 \pm 3.46	91.11 \pm 10.64	92.74 \pm 0.59
<i>Urospora penicilliformis</i> (Uropen)	0.15 \pm 0.03	197.74 \pm 30.59	29.33 \pm 4.80	0.85 \pm 0.03	55.65 \pm 5.38		98.31 \pm 1.21
<i>Ulva intestinalis</i> (Ulvain)	0.15 \pm 0.01	121.33 \pm 26.51	18.62 \pm 4.79	0.66 \pm 0.07	157.25 \pm 41.24	54.81 \pm 4.48	
<i>Ulothrix</i> sp. (Uloth)	0.17 \pm 0.01	260.30 \pm 63.58	44.64 \pm 9.24	0.88 \pm 0.04	32.27 \pm 6.46		
<i>Prasiola crispa</i> (Pracris)	0.18 \pm 0.04	226.74 \pm 15.05	40.82 \pm 11.46	0.50 \pm 0.04	80.5 \pm 5.80	93.73 \pm 14.48	

least 24 h where salinity (33 ± 0.2), conductivity (53 ± 0.2 mS cm^{-1}) and pH (8.3 ± 0.04) were monitored with a portable Multi 350i meters (WTW GmbH, Weilheim, Germany). The system was maintained under a light/dark cycle of 20 h: 4 h and illuminated at $15 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (PAR: 400–700 nm) using TL-D36W/54–765 Daylight lamps (Philips, Amsterdam, The Netherlands).

Photosynthetic characteristics were estimated through electron transport rate vs. irradiance (i.e., P-E) curves. The curves were obtained by exposing the specimens to increasing intensities of PAR from 0 to $446 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ using a pulse amplitude modulation fluorometer (Junior-PAM, Walz, Effeltrich, Germany). Calculations of ETR-E parameters, namely ETR_{max}, initial slope (α) and saturating irradiance (E_k) were performed according to Huovinen and Gómez (2013). Thallus thickness was determined in cross-sections of different fresh collected individuals (or thallus pieces) and measured using light microscopy. The thallus absorbance in laboratory and *in vivo* absorption spectra under solar radiation were determined using a cosine-corrected PAR sensor (Licor 192 SB, Lincoln, USA) and a hyperspectral underwater radiometer RAMSES-ACC-UV (Trios Optical Sensors), respectively, according to Gómez and Huovinen (2011). To determine the area/weight ratio, algae were imaged to scale and afterwards weighed. The surface/area was then calculated using the software Image-Pro Plus 4.55 (Media Cybernetic).

2.4. Estimation of stress tolerance

To determine the stress tolerance to UV radiation and enhanced temperature, specimens of each species were exposed to PAR + UV treatments for 4 h at temperatures of $7 \pm 1^\circ\text{C}$ according to the method described by Flores et al. (2016). Cut-off filters Ultraphan 395

(transmission ≥ 395 nm; Digefra GmbH, Munich, Germany) for PAR control and Ultraphan 295 (transmission ≥ 295 nm; Digefra GmbH) for PAR + UV treatment were used to cover the samples. Irradiance was set at $15 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ for PAR (400–700 nm); 0.26 W m^{-2} for UV-B (280–315 nm) and 1.51 W m^{-2} for UV-A (315–400 nm) using two PAR-emitting tubes (TL-D36W/54–765 Daylight; Philips), which were supplemented with UV-A (UVA-340) and UV-B-emitting tubes (UVB-313) (Q-Lab Corporation, Westlake, OH, USA). The effect of these conditions of UV/T° on photosynthesis (regarded here as a stress tolerance index) was assessed as inhibition of F_v/F_m , which was calculated as the percentage decrease between the value measured in the PAR + UV treatment at 7°C and the value measured in samples exposed to a control condition (PAR at 2°C). The UV doses and temperature conditions used in these exposures have shown to be stressful for a variety of Antarctic macroalgae (Rautenberger et al., 2015).

2.5. Statistical analysis

For analysis the different Antarctic species were grouped in four categorical groups according to (a) taxonomic status: green ($n = 7$), red ($n = 13$), and brown algae ($n = 9$); (b) gross morphology: filamentous ($n = 9$ species), sheet-like ($n = 5$), coarsely branched ($n = 2$), and thick leathery ($n = 13$); (c) depth distribution: intertidal ($n = 11$), shallow sublittoral up to 8 m ($n = 7$), and deep sublittoral between 17 and 30 m ($n = 16$); and d) biogeographical affinity: endemic ($n = 14$), Antarctic-Subantarctic ($n = 10$), broad distribution ($n = 5$).

The relationship between multiple categorical groups and physiological traits (ETR_{max}, α , E_k , absorbance, thickness, area/weight ratios and stress tolerance to UV and temperature (UV/T°) was determined and visualized using correspondence analysis (Greenacre 2007).

Moreover, principal component analysis (PCA) was carried out for the 29 species using the mean values of the different traits grouped in different categorical groups. The factor coordinates of variables and cases, as well as the eigenvalues and variable-factor correlations were estimated using the means for each species. Case scores for PC1 and PC2 were finally compared using one-way analysis of variance (ANOVA) followed by the Tukey HSD post hoc test for unequal N. All the physiological traits were finally correlated with PC1 and PC2 scores using Pearson's product moment analysis. Previous to the analyses, the samples and variables in the data matrix were normalized and standardized according to the routines defined in Statistica (StatSoft Inc.) and Primer 7 (Quest Research Ltd, New Zealand).

3. Results

3.1. P-E curve based photosynthetic variables

The different photosynthetic parameters determined through the ETR vs light curves varied between the different groups of species. The highest values of ETR_{max} close to $44.6 \mu\text{mol e}^- \text{m}^{-2} \text{s}^{-1}$ were measured in the green alga *Ullothrix* sp., while the lowest were recorded in the red alga *Sarcothalia papillosa* ($4.83 \mu\text{mol e}^- \text{m}^{-2} \text{s}^{-1}$; Table 1). The photosynthetic efficiency determined from initial slope of the curve (α) ranged between $0.06 \mu\text{mol e}^- \text{m}^{-2} \text{s}^{-1} (\mu\text{mol m}^{-2} \text{s}^{-1})^{-1}$ in the red alga *Curdiea racovitzae* and *Plocamium cartilagineum* and $0.24 \text{e}^- \text{m}^{-2} \text{s}^{-1} (\mu\text{mol m}^{-2} \text{s}^{-1})^{-1}$ in the brown alga *Desmarestia menziesii* (Table 1). The light requirements for saturation of photosynthesis (E_k) reached values of $260 \mu\text{mol m}^{-2} \text{s}^{-1}$ in *Ullothrix* sp., while the brown alga *Cystosphaera jacquinotii* was the species with the lowest E_k values averaging $36 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 1). These ranges in E_k match the prevailing light conditions in the water column at King George Island. An exercise assuming a surface irradiance of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ under K_d for PAR of 0.15m^{-1} indicated that the highest E_k values of intertidal species and the lowest E_k values of subtidal algae fall in a range of depths between 9 and 22 m, respectively (Fig. 3).

3.2. Bio-optical and morpho-functional traits

The *in vivo* spectral absorbance patterns of various Antarctic macroalgae indicated a relationship between thallus absorbance, thickness and algal taxonomy (Fig. 4). As a consequence of a low absorption of

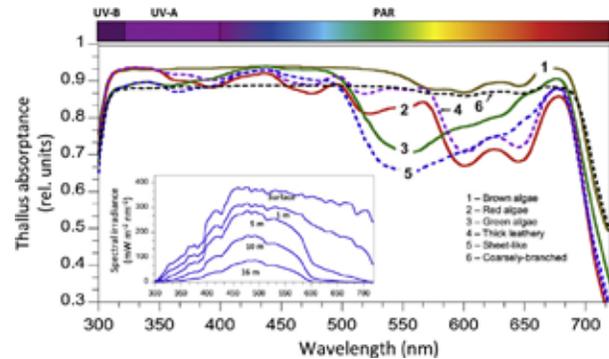


Fig. 4. *In vivo* absorbance spectra of Antarctic macroalgal species averaged according to algal taxonomy and morphology. The spectral irradiance at different depths indicating the prevalence of the biologically relevant wavelengths is indicated. Values represent means of three profiles in each depth.

chlorophylls in delicate morphs, mostly green algae, e.g. *Monostroma* and *Ulva* attaining thallus thickness $< 500 \mu\text{m}$, reduced absorbance by approximately 35% at wavelengths of 500 to 650 nm was shown. In red algae with thick leathery characteristics (e.g. *Iridaea*, *Gigartina*), absorbance decreased at wavelengths between 600 and 680 nm. The highest absorbance across the whole wavelength range was found in brown and coarsely branched algae (Fig. 4). The frequency distribution of thallus absorbance varied in average between 0.49 and 0.7 in sheet-like morphs, while in coarsely-branched algae upper range means were close to 0.93 (Fig. 5A). The highest values of area/weight ratio (1:10) were found in sheet-like algae (Fig. 5B), whereas the lowest ones were determined in thick-leathery morphs, which also attained the thicker thalli. In filamentous and sheet-like algae, thallus thickness was $< 600 \mu\text{m}$, whereas CB and TL algae reach thallus thicknesses of 1000 and 2000 μm , respectively (Fig. 5C).

3.3. Sensitivity to UV and temperature stress

The studied species showed in general a high tolerance to UV radiation and temperature (7°C). Decrease in F_v/F_m was around 39.6% in the red alga *Curdiea racovitzae* from the subtidal zone, while specimens of the Rhodophyta *Iridaea cordata* from of intertidal and shallow subtidal populations were the most tolerant (Table 1). When species were grouped by algal taxonomy or gross morphology, no differences were found in the tolerance of algae to UV and temperature stress ($p > 0.05$; Fig. 6). However, significant differences were detected in algae from different depths and those with Antarctic-Subantarctic distribution, which had contrasting patterns: while algae from deep sublittoral zones were more affected by stress than their counterparts from shallower locations, species with Subantarctic and endemic affinity were less affected ($p < 0.05$; Fig. 6).

3.4. Patterns based on multivariate analysis

PCA analysis indicated that PC1 and PC2, with eigenvalues of 3.31 and 1.77, respectively, accounted by 63.5% of the whole variability in all the studied traits (Fig. 7). From the 2-D plot and the eigenvectors we could infer that PC1 is related with light absorption characteristics separating green algae from brown and red algae, which is defined by increasing E_k , ETR_{max} and area/weight ratio, and decreasing thickness and absorbance. On the PC2, the analysis revealed that red algae are well discriminated from brown algae based on decreasing photosynthetic efficiency (α), and tolerance to UV/ T° and to less degree on size (Fig. 7). These patterns were confirmed by the correspondence analysis where three major clusters of algae were identified along two dimensions, which accounted for 47% of the total inertia (Fig. 8). Here, dimension 1 separated broad distributed green algae attaining sheet

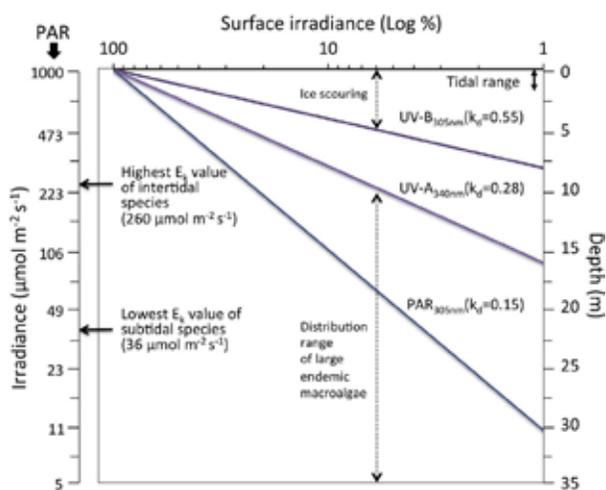


Fig. 3. Vertical profile of underwater solar radiation and vertical attenuation coefficients (K_d in m^{-1}) for wavelengths of UV-B and UV-A radiation and PAR (400–700 nm) measured in Fildes Bay during clear sky (mean of four measurements). The left axis represents an example of underwater light (PAR) scenario using a surface irradiance of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ to indicate as a reference the depth ranges of solar radiation that set photosynthetic light demands (E_k).

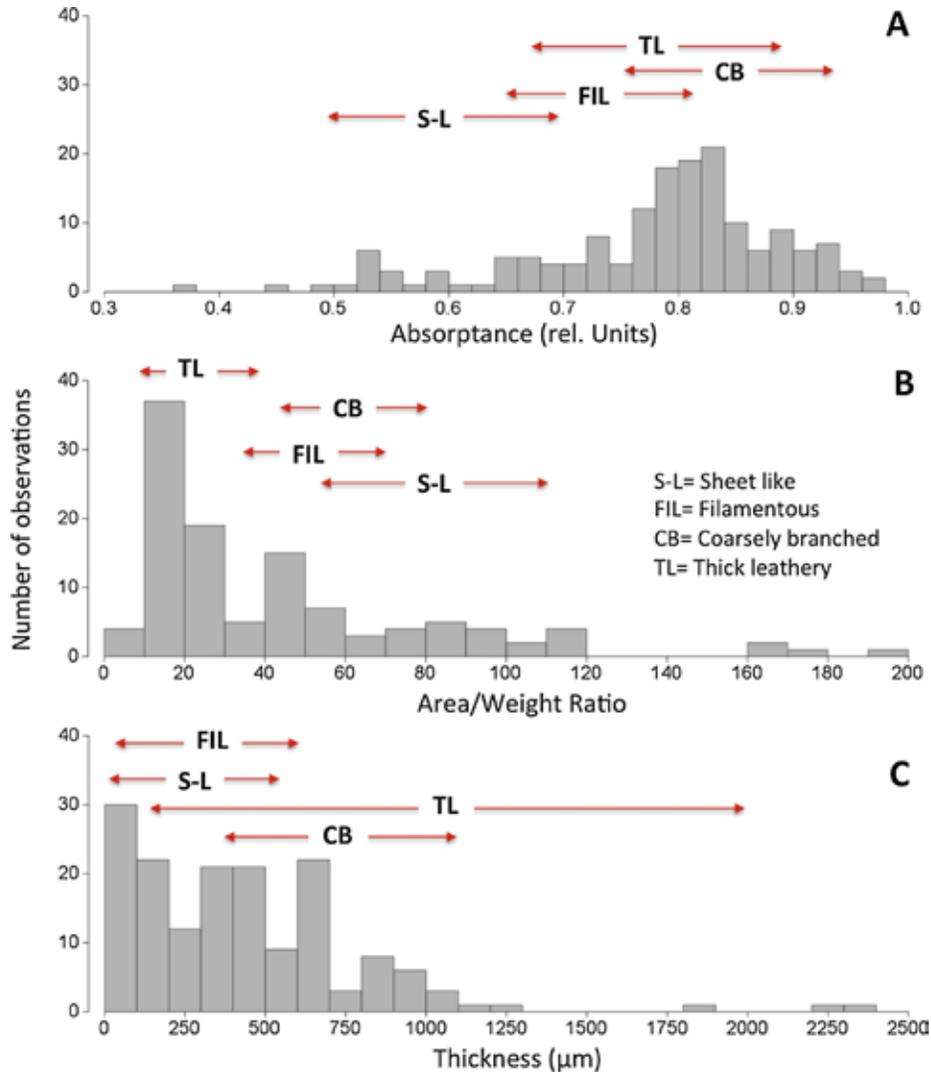


Fig. 5. Frequency distribution of morpho-functional traits (absorbance, area/weight ratio and thickness) across different gross morphologies considering all the studied algae. Ranges for each morphology represent average for each species.

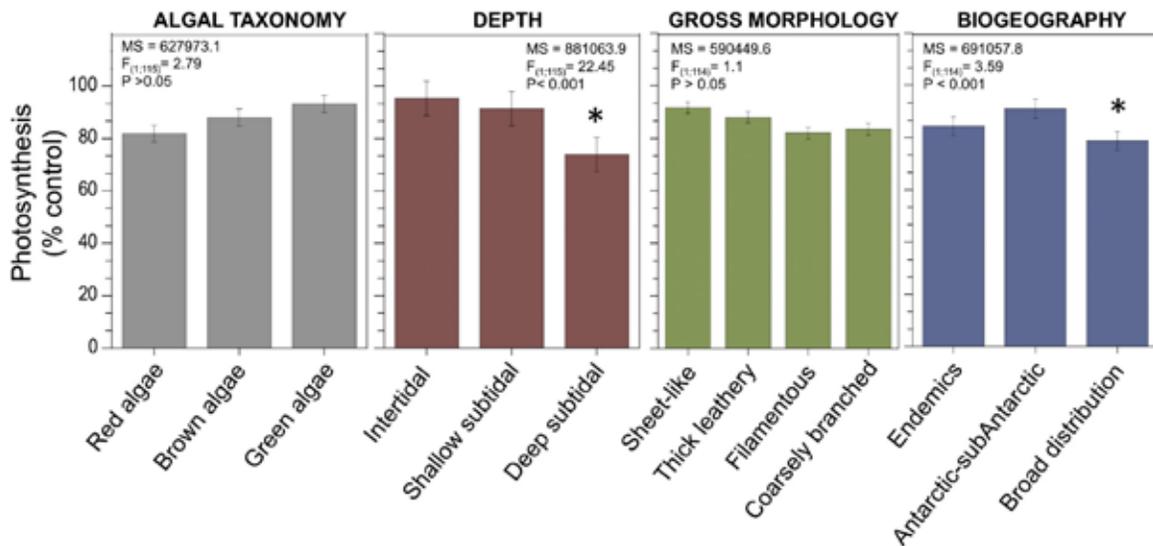


Fig. 6. Tolerance of photosynthesis measured as maximal quantum yield (F_v/F_m) after a 4-h UV exposure under enhanced temperature (7°C). Values are averages according to algal taxonomy, depth gross morphology and biogeography. Results of one-way ANOVA and significances (*) are indicated.

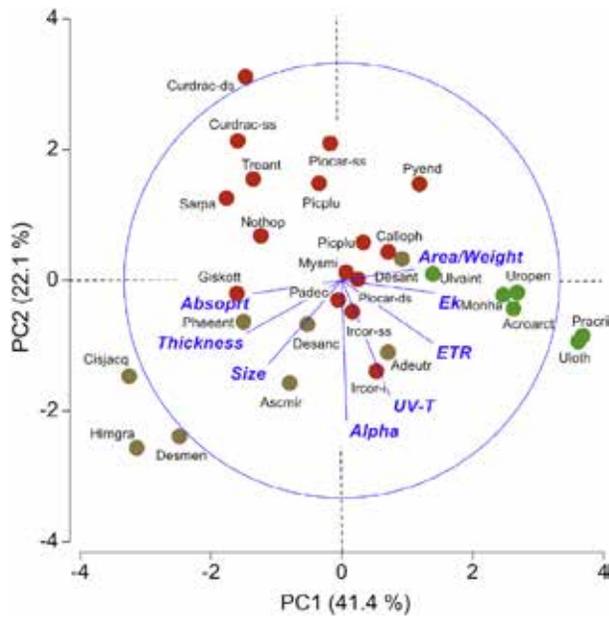


Fig. 7. Principal component analysis (PCA) plots of eight functional traits from 29 species of Antarctic macroalgae. Dots represent species from red, green and brown algae. Abbreviations of species names are indicated in Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

like and filamentous morphs from endemic brown algae inhabiting deep locations, which normally exhibit coarsely branched morphology. Dimension 2 discriminated seaweeds with Antarctic-Subantarctic origin, normally red algae inhabiting shallow waters and with thick leathery characteristics. Analysis of variance performed on PC1 and PC2 case scores indicated that the algal assemblages were defined significantly ($p < 0.05$) by algal taxonomy, depth, morphology and biogeographic affinity. In contrast, PC2 scores varied significantly only in terms of algal taxonomy ($p < 0.05$; Table 2). When the physiological traits were plotted against PC1 and PC2 scores, some significant relationships could be established: PC1 was correlated with variables related with bio-optical properties, e.g. negatively with absorptance

Table 2
Results of one-way ANOVA for factor scores PC1 and PC2 estimated using PCA.

Source	SS	D.F.	MS	F	p
PC1					
Algal group	37.57	2	18.78	11.19	0.0006
Error	31.88	19	1.67		
Depth	36.72	2	18.36	10.65	0.0007
Error	32.74	19	1.72		
Morphology	33.91	3	11.31	5.72	0.006
Error	35.54	18	1.97		
Biogeographic affinity	33.04	2	16.52	8.61	0.002
Error	36.41	19	1.92		
PC2					
Algal group	12.67	2	6.33	5.13	0.02
Error	23.44	19	1.23		
Depth	3.14	2	1.57	0.90	0.42
Error	32.96	19	1.73		
Morphology	1.69	3	0.56	0.29	0.82
Error	34.42	18	1.91		
Biogeographic affinity	0.90	2	0.45	0.24	0.78
Error	35.21	19	1.85		

and thickness and directly with E_k PC2 scores related significantly with alpha (an indicator of photosynthetic efficiency) and the tolerance to UV radiation and temperature (Fig. 9).

4. Discussion

Our framework based on the categorization of functional traits of 29 macroalgal species from Fildes Bay (West Antarctic Peninsula) allowed determining some general tendencies. Bio-optical related traits, e.g. absorptance, thickness, area/weight ratio and size were arranged along a depth gradient, while other parameters such as photosynthetic efficiency (α) and ETR_{max} had lower predictive value in terms of depth distribution. Stress tolerance capacity, which was grouped together with P-E curve parameters in the PCA analysis, varied in relation with depth and biogeographic affinity, but was not linked to gross morphology. Based on the whole set of functional traits, the correspondence analysis identified three major clusters with strongly superimposed categorical trait groups: a group of species was integrated by little filamentous and sheet-like green algae, normally widely distributed and inhabiting almost exclusively at the intertidal zone; a second cluster

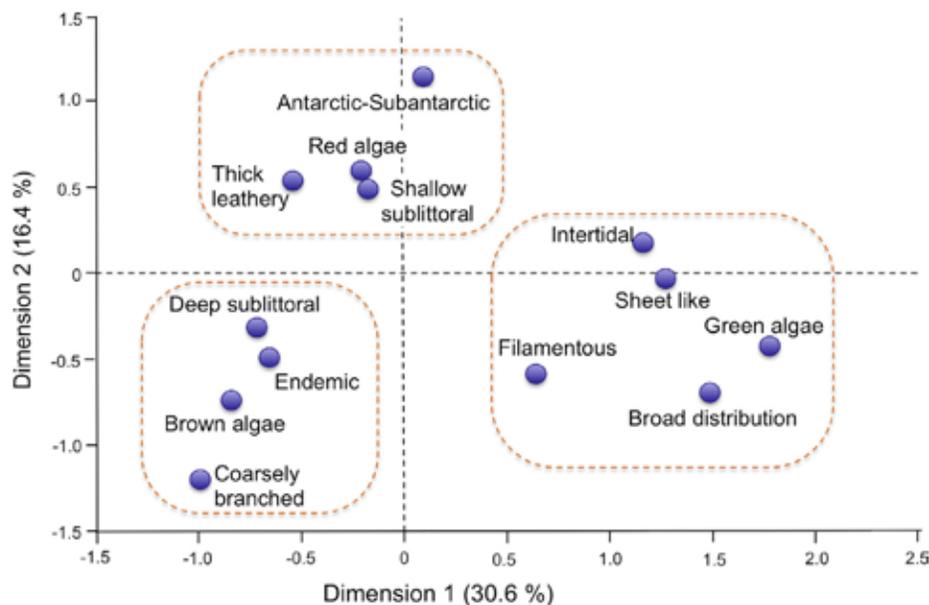


Fig. 8. Plots of coordinates of multiple correspondence analysis for eight functional traits integrated in different categorical clusters.

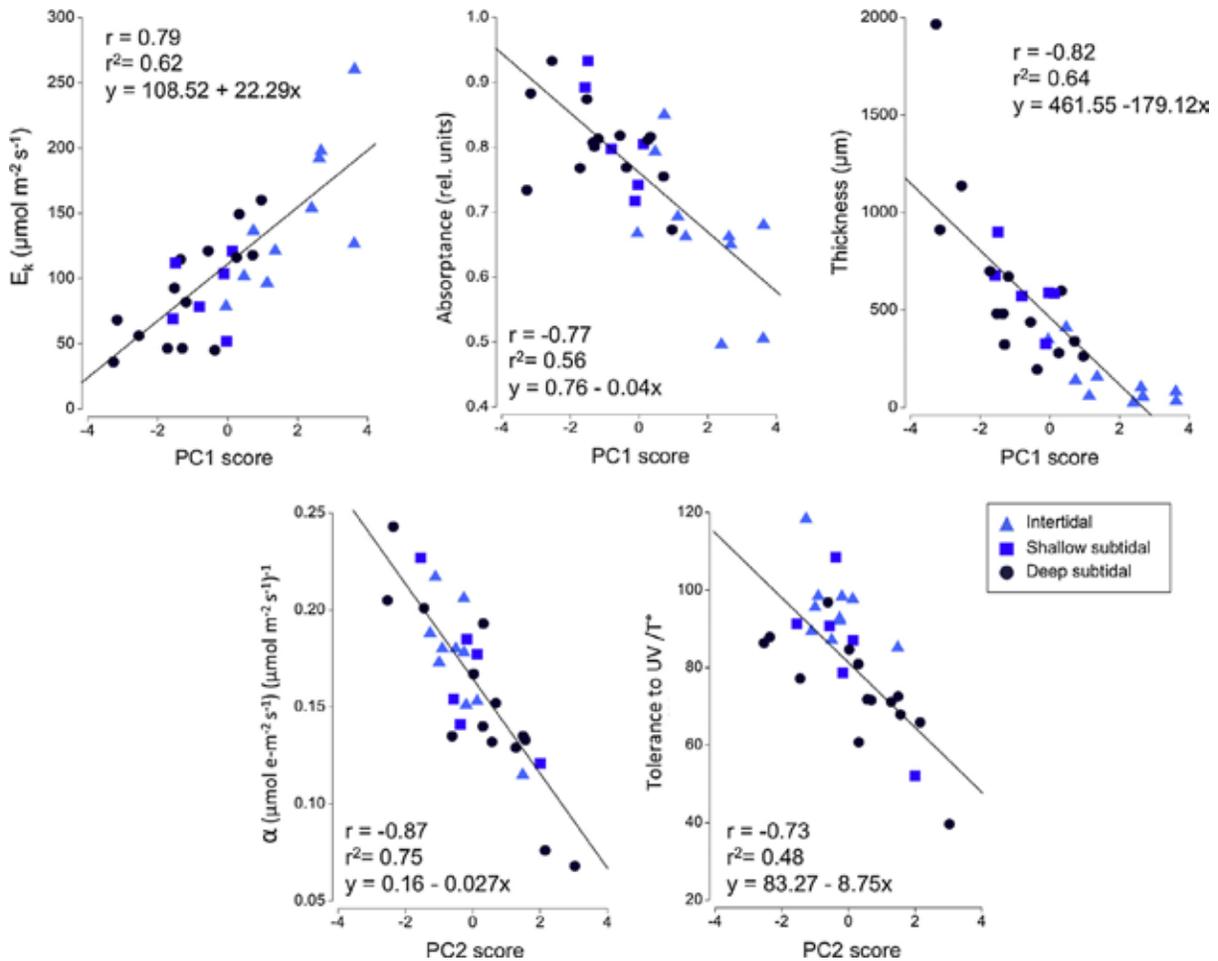


Fig. 9. Relationship between PC1 and PC2 scores from PCA with various functional trait data along a depth gradient. Pearson, regression coefficients and linear equation are indicated. Symbols represent different depth strata where algae were collected.

was defined by large canopy-forming brown algae, which are obligated subtidal species and endemic to Antarctica; and finally a third assembly of species represented mostly by shallow sublittoral red algae attaining Antarctic-Subantarctic distribution. Furthermore, this study provides further evidence on the effect of UV exposure on macroalgae, which was associated mainly to the depth distribution, but not to gross morphology.

4.1. Light use and bio-optical characteristics

Probably the most distinctive trait of Antarctic macroalgae is their remarkable photosynthetic efficiency at very low light levels (Gómez et al., 2009). In the present study the photosynthetic characteristics based on P-E curves of Antarctic macroalgae confirmed that the species are shade-adapted, which is an important pre-requisite for survival during long periods of dim light and metabolically able to occupy broad light gradients (Weykam et al., 1996; Huovinen and Gómez, 2013; Gómez and Huovinen, 2015). Despite the wide variation in E_k ($36\text{--}260\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$) between species, and between groups of species, a consistently high photosynthetic efficiency (α_{ETR}) across the entire range of depth was found. This contrast with the high light penetration ($Z_{1\%}$ for PAR close to 30 m) in this zone, which permit irradiances close to $50\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ at 20 m depth during clear summer day (Huovinen et al., 2016). Under these conditions, photosynthesis and growth of endemic species, in particular large brown algae of the order Desmarestiales and understory red algae is not constrained at considerable depth (Drew, 1977; Weykam et al., 1996; Schwarz et al., 2003;

Huovinen and Gómez, 2013).

Bio-optical traits associated with thickness, absorbance, area/weight ratios and size resulted to be good predictors to classify macroalgae in terms of their light use characteristics and hence their depth distribution. Although variability in these functional characteristics is scattered over different groups of species, it is possible to recognize some patterns: in general, the green algae (e.g. genera such as *Urospora*, *Ulva* or *Ulothrix*), in virtue of their obvious differences in light absorption capacity, thallus thickness and size, were clearly discriminated from large leathery and coarsely forms. For instance, the filamentous and sheet-like green algae living at intertidal zones showed the lowest values of absorbance in almost all wavelengths when compared to red and brown algae, but mainly in the green region ($\sim 500\text{--}570\ \text{nm}$). These differences could be a consequence of a low absorption of chlorophylls at these wavelengths or could be influenced by the composition and content of photosynthetic pigments, by package effect, and even by the algal morphology and photosynthetic capacity (Gómez and Huovinen 2011). For instance, the absorbance in thick leathery species, mostly red algae, decreased in wavelengths between 600 and 670 nm due to lower absorption of phycobiliproteins. Similar relationship was previously reported in algae from Potter Cove, King George Island Weykam et al. (1996), southern Chile (Gómez and Huovinen 2011) and Gullmar Fjord in the Baltic Sea (Johansson and Snoeijis 2002).

4.2. Can functional traits be indicative of life history strategies?

Kain in 1989 categorized macroalgal species in two major groups, “season responders” and “season anticipators”, according to their capacity to “manage” the seasonality. She defined that season responders show an opportunistic life strategy and start growth and reproduction during favorable light conditions. In contrast, growth and photosynthesis in season anticipators is not necessarily dependent on the seasonality. The concept was followed by Wiencke (1990), who determined that Antarctic macroalgae can be assigned to these two classifications. Due to the sharp environment gradients along the depth profile in Antarctica, it would be reasonable to argue that “season responders” are more suited to thrive in highly changing shallow/intertidal zones, while “season anticipators” could have advantages at deeper locations. In our study, the season responders (e.g. *Ulva intestinalis*, *Acrosiphonia arcta*, *Monostroma hariotti*, *Urospora penicilliformis*, *Adenocystis utricularis*) are characterized by small size, rapid growth and turnover rate and thin morphology. In fact, this life strategy is rewarding to endure the changing environment at the intertidal zone, and the phenology and abundance of these species is strongly tuned with the oscillations in environmental conditions (Marcías et al., 2017). Moreover, other species with thick leathery morphology e.g. the red algae *Iridaea cordata* and *Gigartina skottsbergii*, show season responder characteristics and also exhibit rapid photosynthetic adjustments to respond to the changing environment (Weykam et al., 1997; Wiencke et al., 2007). Using the definitions proposed by Grime (1981) for terrestrial vegetation, this group of macroalgae could correspond to the “ruderal” species, which are permanently subjected to strongly physical perturbation. Apparently the relationship between life-history traits conferring advantages under high levels of disturbance is convergent in different types of littoral assemblages as was outlined by Steneck and Dethier (1994) in their functional-group model.

In contrast, season anticipators (e.g. *Desmarestia menziesii*, *D. anceps*, *Himantothallus grandifolius*, *Ascoseira mirabilis*, *Trematocarpus antarcticus*, *Phyllophora ahnfeltioides*, *Palmaria decipiens*) starting growth in late winter/spring, frequently under the sea-ice, are generally perennial species with a development and phenology closely tuned with the Antarctic daylength regime (Wiencke, 1990; Wiencke et al., 2007). These characteristics together with large and massive gross morphology (e.g. leathery, coarsely branched, etc.) are closely related with thicker fronds, enhanced light absorbance and low area/weight ratio, confer advantages to survive several years under limited light conditions at deeper locations. Moreover, these traits are functional to withstand physical perturbations (e.g. ice scouring, grazing), to outcompete other benthic organisms (Olson and Lubchenco, 1990) and in general, can be regarded as key factors defining the stability of the whole benthic community as ecosystem engineers (Valdivia et al., 2015; Ortiz et al., 2016). In the terrestrial model these algae would be equivalent to those groups of plants defined as “competitive strategists” (sensu Grime, 1981). In the case of endemic Desmarestiales, large size implicitly can be related with a series of morpho-functional adaptations, e.g. a metabolic carbon balance set to use very low light conditions (Gómez et al., 1997; Deregibus et al., 2016) or the remobilization of storage carbohydrates to power the frond elongation by the intercalary meristem (Gómez et al., 1998). Similar photobiological adaptations have evolved in understory red algae (e.g. *Myriogramme*, *Plocamium*, *Callophyllis*) despite they do not display a massive thallus architecture. Instead, these species are extremely shade adapted in virtue of their very low light requirements for photosynthesis and high concentrations of photosynthetic pigments (Gómez et al., 2009).

4.3. Functional traits in the context of a changing polar environment

In the context of the global warming, which is affecting large coastal regions especially around the Western Antarctic Peninsula (Clarke et al., 2012), the functional responses of macroalgae strongly influence

biomass accrual and species richness, which are important for predicting the community responses (e.g. resilience) to present and future environmental shifts (Isbell et al., 2015; Valdivia et al., 2015; Jänes et al., 2016). In fact, macroscopic properties modeled for Fildes Bay, King George Island, indicate that Antarctic ecosystems are less developed than benthic ecosystems from temperate regions e.g. estuaries and coral reefs, however, they could more resistant to disturbances (Ortiz et al., 2017).

Although Antarctic macroalgae exhibited high tolerance to UV and temperature (> 70%), our study permitted to identify deep subtidal algae as more sensitive ($p < 0.05$) to environmental stress, at least within a short-term time span. In many cases, both groups showed some differences in gross morphology, taxonomic status and biogeographic affinity. The PCA analysis identified well these patterns indicating that tolerance traits are strongly related with photosynthetic traits. The high stress tolerance of intertidal species (mainly delicate morphs) lies in the fact that they are frequently exposed to e.g. high UV radiation, especially during very low tides, in spring-summer season (Richter et al., 2008; Huovinen and Gómez, 2013). Based on pure optics, delicate intertidal macroalgae attaining delicate thalli might, intuitively, be regarded as highly sensitive to UV damage. Despite the basis relating stress tolerance and gross morphology are not well understood, in general, delicate morphs exposed to persistent solar and thermal stress can be acutely affected, however, they show efficient recovery capacity displaying a suite of photoprotective and anti-stress mechanisms (Bischof et al., 2002; Cruces et al., 2013). In general, studies carried out in Antarctic intertidal green algae indicate that they are highly UV tolerant (Bischof et al., 1998; Gómez et al., 2004; Rautenberger and Bischof, 2006). In many cases this tolerance relies on morpho-functional processes as has been reported for the filamentous green alga *U. penicilliformis*. This species is highly insensitive to high solar radiation in virtue of a dense cell wall, presence of mucilage and external mineral deposition providing an efficient UV shielding (Roleda et al., 2010). Another important morphological adaptation is the formation of mats or turf-like structures that are effective to minimize the UV injury on the whole organism (Bischof et al., 2006). This corroborates that Antarctic representatives of this group, probably recent invaders, have retained a physiological ability to cope with extreme physical conditions at the intertidal zone (Wiencke and Clayton, 2002).

Especially remarkable is the high stress tolerance recorded for endemic Antarctic species living at deeper locations, which is related to a combination of bio-optical and physiological adaptations. With a thick, multilayered architecture, which is associated with enhanced absorption of PAR over a broad depth range, these algae minimize the impact of harmful UV radiation by increasing thallus cross section (low area/weight ratio) and ultrastructural compounds, thus scattering the number of quanta reaching target molecules (Ramus, 1981). Although UV photoprotection by morphological traits is strongly overlapped by other factors related with gross morphology, e.g., size scape from grazers, overgrowth, competition for space, etc. (Olson and Lubchenco, 1990), apparently there is a trade-off between highly efficient light absorption properties and tolerance to UV radiation, which is mediated by the synthesis and accumulation of phenolic compounds (Gómez and Huovinen, 2015; Flores-Molina et al., 2016). Although phenolics (phlorotannins) in Antarctic large brown algae respond to different biotic and abiotic factors (e.g. grazing, temperature, UV radiation) (Amsler et al., 2005; Iken et al., 2009; Huovinen and Gómez, 2013; Rautenberger et al., 2015), these substances are essential in the polymerization of the cell wall, and hence directly connected with biomass formation processes (Schoenwaelder, 2002).

Two of the most important consequences of ocean warming is the reduction of sea ice cover and the retreat of glaciers with important alterations in light, salinity, sedimentation and various physical processes (Braun and Grossmann, 2002). A shorter period and thinner layers of the sea ice cover allow deeper light penetration, and can influence not only changes in the acclimation of macroalgal

photosynthesis (Runcie and Riddle, 2007) and enhanced impact of UV radiation (Fountoulakis et al., 2014), but also a downward shift in patterns of development and colonization of benthic algae (Campana et al., 2009; Clark et al., 2017). For example, in eastern Antarctica, abundant canopy-forming macroalgae were found at sites where sea-ice cover break-up occurs during spring, but they were absent at sites that retained ice cover until summer (Johnston et al., 2007). In the case of glacier retreating, new ice-free areas, characterized by enhanced sediment input, could be suitable for macroalgal colonization only if these species show efficient adaptations to photosynthesize and growth to very low light conditions (Quartino et al., 2013). Due to that canopy-forming endemic brown algae show positive carbon balance to depths as high as 30 m (Gómez et al., 1997), the turbid conditions caused by glacial run-off will elevate the lower limits of vertical distribution of these species (Deregibus et al., 2016). Moreover, near the glaciers disturbance caused by ice scouring can considerably affect the benthic community structure (Smale, 2008). For example, the presence of different canopy-forming algae and their development status can be regarded as suitable proxies to examine the degree of ice disturbance as well as the successional state of the community (Clark et al., 2011). In a similar manner as for key plant groups in terrestrial ecosystems (Kominoski et al., 2013), the notion that large macroalgae supporting structure and function of Antarctic coastal benthic communities can ameliorate the impact of physical stress has been recently examined (Valdivia et al., 2015; Ortiz et al., 2016, 2017). These studies suggest that canopy forming species across a broad vertical profile, provide stable environmental conditions for other benthic organisms, including understory species, and are involved in facilitative interactions due to their key functional traits (e.g. ecosystem engineers), which finally determine resource complementarity, species richness and community biomass (Valdivia et al., 2015). In this way, it seems that the ecosystem dominated by large macroalgae counts for internal mechanisms operating at individual (i.e. efficient morpho-functional and anti-stress mechanisms) and community (i.e. high biological complexity) levels that provide the system with a high resistance to disturbances caused by the Antarctic environment (Ortiz et al., 2016, 2017).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.pocan.2018.03.013>.

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