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RESEARCH/REVIEW ARTICLE

Adjustment of pigment composition in *Desmarestia* (Desmarestiaceae) species along a sub-Antarctic to Antarctic latitudinal gradient

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Abstract

Photosynthesis at high latitudes demands efficient strategies of light utilization to maintain algal fitness and performance. The fitness, and physiological adaptation, of a plant or algae species depends in part on the abundance and efficiency of the pigments it can produce to utilize the light resource from its environment. We quantified pigment composition and concentration in six species of the brown macroalgal genus *Desmarestia,* collected from sub-Antarctic sites (Strait of Magellan, Beagle Channel–Cape Horn Province) and sites on the Antarctic Peninsula and adjacent islands. Sub-Antarctic *Desmarestia* species exhibited lower concentrations of chlorophyll *a*, chlorophyll *c* and fucoxanthin than endemic Antarctic species. Antarctic samples of *D. menziesii* and *D. antarctica* collected along a decreasing latitudinal gradient showed spatial and interspecific differences in light-harvesting pigment composition. Our results suggest distinct physiological adjustments in *Desmarestia* species in response to heterogeneous abiotic environmental conditions. The marine sub-Antarctic and Antarctic ecosystems are characterized by harsh environments (e.g., extreme irradiance, photoperiod, temperature, salinity) to which the physiology of macroalgal species must adapt.

The Chilean sub-Antarctic ecoregion of Magallanes (or Magellan) hosts a coastal, benthic community that is highly distinct from other temperate rocky shores on the South American Continent in terms of species composition, richness and structure. Such distinctions could be the result of several factors, such as the geomorphology generated by the glacial erosion during the advance and retreat of ice in the Quaternary (Silva & Calvete 2002); oceanographic gradients combining unique current flows, salinity, and thermal (Dayton 1985; Silva & Calvete 2002), photoperiod and irradiance regimes; presence of glaciers with predominant west-to-east gradients of winds and rainfall (Aravena & Luckman 2009) and freshwater coastal discharge; variable substrate types with abrupt change in geomorphology of the sub-Antarctic system of fjords and channels (Valdenegro & Silva 2003), resulting in unique physical and biogeochemical seawater conditions (e.g., nutrient cycles, carbonate system dynamics [Torres et al. 2014]) that generate a distinct algal structure. The environmental heterogeneity governing sub-Antarctic and Antarctic coastal ecosystems has shaped the evolutionary history and physiological adaptations of the local macroalgal flora.

From phylogenetic, morphological and eco-physiological studies of the genus *Desmarestia* (Lamouroux 1813) conducted in the Antarctic ecoregion of Magallanes, it was

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Abbreviations in this article
chl *a*, *b*, *c*: chlorophyll *a*, *b*, *c*
Fucox: fucoxanthin
FW: fresh weight
PAR: photosynthetically active radiation

found this species originated from an Antarctic ancestor, then radiated north, eventually reaching the Northern Hemisphere through long-distance natural dispersal (Peters et al. 1997). Within the sub-Antarctic Chilean ecoregion of Magallanes, the genus *Desmarestia* is represented by *D. confervoides* (Bory de Saint-Vincent) M.E. Ramírez & A.F. Peters, *D. chordalis* J.D. Hooker & Harvey and *D. ligulata* (Stackhouse) J.V. Lamouroux. Currently, *D. distans* and *D. muelleri* are considered subspecies of *D. ligulata* (Setchell & Gardner 1925; Guiry & Guiry 2014; Yang et al. 2014).

The representative *Desmarestia* species in the Antarctic continent are *D. anceps* Montagne, *D. menziesii* J. Agardh (Lamb & Zimmermann 1977; Wiencke et al. 1995) and *D. antarctica* Silva & Moe (Moe & Silva 1989; Wiencke et al. 1991). These *Desmarestia* species, together with *Himantothallus grandifolius* (A. Gepp & E.S. Gepp) A.D. Zinova (1959), comprise a large proportion of the macroalgal biomass along the Antarctic Peninsula (Amsler et al. 1995; Brouwer 1996; Quartino et al. 2001; Quartino et al. 2005), yet are largely understudied despite supporting a diverse, associated floral and faunal community.

Photosynthetic pigment composition can reveal potential adaptation and acclimation success, and the physiological traits of macroalgae (Motten 1995; Plastino & Mansilla 2004). A species' reaction to the given radiation climate is determined by the interaction between genetic adaptation and physiological acclimation where adaptation must precede acclimation to changing environmental conditions (Bischof et al. 2006). That is, the species-dependent and variable genetic preadaptations to limiting, but also potentially harmful, radiation would shape its physiology in the natural environment. For example, in *Lessonia nigrescens* of the Southern Hemisphere, the photosynthetic responses to seasonally changing irradiance levels are some of its adaptations, along with its ontogenic development (Huovinen et al. 2006). Pigment composition is frequently used as a biomarker to infer physiological adaptations of plants and algae (e.g., Dring 1981; Ramus 1983) to differing environmental variables across bioregions (Falkowski & LaRoche 1991). *Laminaria saccharina*, for instance, may be capable of optimizing photosynthesis over a wide range of light levels by complex metabolic regulation (Machale et al. 1996). And, under variable irradiance, the red algae *Gracilaria lemaneiformis* showed differential vegetative and physiological strategies to adapt to environmental stress by regulating different metabolic processes (e.g., photosystem II reaction centres normalization; Wu et al. 2015). The biochemical reactions of photosynthesis are directly coupled to light availability (Plastino & Mansilla 2004), and the respective share of chl *a* as reaction centre pigment to chl *c* and other accessory pigments, such as the xanthophyll Fucox, may reveal adaptive responses towards heterogeneous light and climate, fluctuating with latitude, depth, season or a combination of all (Mansilla & Alveal 2004; Plastino & Mansilla 2004). In addition to irradiance and photoperiod (hours daylight: hours darkness), temperature, salinity and nutrients may be further limiting factors at high latitudes, affecting the efficiency of light capture for photosynthesis.

Our objectives were to examine (1) the adjustments or intraspecific differences in pigment composition and ratio (chl *c*/chl *a*; chl *c*/Fucox) in species of the genus *Desmarestia* spatially from sub-Antarctic to Antarctic marine habitats and (2) the intraspecific differences in pigment concentration in two Antarctic species within the genus *Desmarestia* (*D. antartica*, *D. menziesii*). We hypothesized that primary (chl *a*) and accessory (chl *c* and Fucox) pigment composition in *Desmarestia* species will differ among sites along the latitudinal gradient of sub-Antarctic to Antarctic waters; and along the Antarctic Peninsula, despite site proximity and past connectivity, reflecting response to local conditions such as different duration and intensity of solar irradiance between regions. The overall results of this investigation will contribute to current knowledge and understanding of macroalgal eco-physiology. Marine photosynthetic physiology in sub-Antarctic and Antarctic irradiance regimes is likely to become increasingly relevant in the context of present and future global changes.

Materials and methods

Study sites

Two sites in Chile's sub-Antarctic region and eight sites along the Antarctic Peninsula were selected to represent a range of environmental conditions (Table 1). We used a Solar Light® radiometer (model: PMA 2200) and a Yellow Spring Instrument® handheld multiparameter (model: MPS) at some sites (e.g., Saint Ana) or a conductivity–temperature–depth recorder (SBE 19plus V2 SEACAT Sea-Bird Electronics Inc.) measurements to first 10 m depth at other sites (e.g., Deception). When not available, approximates of environmental data were obtained from published literature for the given site (e.g., Santana et al. 2006; Clarke et al. 2008; Smith & Comiso 2008; CEAZA-MET 2010; Table 1).

Table 1 Environmental and habitat variables registered in 2011, 2012 and 2013 during collection of five *Desmarestia* species at 10 study sites in sub-Antarctica and Antarctica. Shown are the mean or mean range values.

Desmarestia species name	Study site	Depth (m)	PAR (µE /m^{2}s)	Salinity (psu)	Temperature (°C)	Dissolved O$_2$ (mg/L)	Habitat substrate type
Sub-Antarctica							
D. confervoides	St Ana Point	5–7	526.4	32.53	9.73	12.8	Cliff
D. ligulata subsp. *ligulata* f. *distans*	St Ana Point (S53°08′; W71°00′)	5–7	526.4	32.53	9.73	12.8	Cliff
D. ligulata subsp. *muelleri*	St Ana Point	5–7	526.4	32.53	9.73	12.8	Cliff
D. confervoides	Paula Bay	5–7	164–165	32.17	4.7–10.9	–	Boulders
D. ligulata subsp. *ligulata* f. *distans*	Paula Bay (S54°55′; W67°55′)	5–7	164–166	32.17	4.7–10.9	–	Boulders
D. ligulata subsp. *muelleri*	Paula Bay	5–7	164–167	32.17	4.7–10.9	–	Boulders
Antarctica							
D. antarctica	Fildes (S62°12′; W58°54′)	5–7	729–787	34	2	10.9	Cliff
D. menziesii	Fildes	5–7	729–787	34	2	10.9	Cliff
D. anceps	Prat (S62°27′; W59°44′)	9–12	748–768	33.85	2.1	8.0	Boulders
D. menziesii	Prat	5–7	748–768	33.85	2.1	8.0	Cliff
D. antarctica	Prat	5–7	748–768	33.85	2.1	8.0	Boulders
D. anceps	Hanna (S62°39′; W60°37′)	10	729–787	34	1.8	7.1	Cliff
D. antarctica	Hanna	5–7	729–787	34	1.8	7.1	Cliff
D. menziesii	Deception (S62°59′; W60°35′)	5–7	901.21	33.87	2.1	8.0	Boulders
D. antarctica	Deception	5–7	901.21	33.87	2.1	8.0	Rocky shore
D. antarctica	Spring (S64°17′; W61°05′)	5–7	729–787	33.4	0–1	–	Cliff
D. menziesii	Spring	5–7	729–787	33.4	0–1	–	Cliff
D. menziesii	Argentine (S65°14′; W64°15′)	5–7	729–787	33.4	0–1	–	Cliff
D. menziesii	Rothera (S67°33′; W68°07′)	5–7	1005.9	33.29	1.72	12.6	Cliff
D. menziesii	Carvajal (S62°12′; W58°54′)	5–7	739.6	32.59	0.24	13.3	Cliff
D. antarctica	Carvajal	5–7	739.6	32.59	0.24	13.3	Rocky shore

Field sample collection

Fronds of *Desmarestia confervoides* and the subspecies *D. ligulata* subsp. *ligulata* f. *distans* and *D. ligulata* subsp. *muelleri* were collected in the austral summer period (December 2011–February 2012) at two sites along the Strait of Magellan to the Beagle Channel (Table 1; Fig. 1). *D. antarctica, D. menziesii* and *D. anceps* were collected in Antarctica by scuba diving in February 2013 off Fildes Bay (Fildes), Hanna Point (Hanna), Prat Point (Prat), Deception Island (Deception), Spring Point (Spring), Argentine Islands (Argentine), Rothera Base (Rothera; except *D. antarctica*, not found) and Carvajal Base (Carvajal; Table 1, Fig. 1). All specimens were placed in freeze–cooler containers to prevent sulfation of *Desmarestia* individuals and/or degradation of pigments from exposure to light and temperature changes. Sub-Antarctic samples were processed upon collection immediately at the Laboratory of Antarctic and sub-Antarctic Marine Ecosystems, University of Magallanes, in Punta Arenas, Chile. Antarctic samples were transported in coolers, over the short 5- to 10-min Zodiac ride back to our research vessel where they were frozen at −25°C to avoid loss of pigment or similar deterioration for later analysis at the laboratory.

Pigment analyses

Seven random, individual samples of each species of *Desmarestia* ($7\,\mathrm{n} \times 6$ species $= 42$) were taken to the laboratory. The frozen samples were thawed, washed with sterilized seawater of salinity 34 psu and were carefully brushed to remove epiphytic organic material. Random ca. 2 cm^2 subsamples (0.125 g FW) from the fronds were gently patted with paper towel to remove excess water and weighed in a Radwag analytical balance (AS 220/c/2) for pigment analysis (Seely et al. 1972). Our prior work (unpublished) and that of Seely et al. (1972) showed that dimethyl sulfoxide readily extracts pigments without further addition of acetone. One mL of dimethyl sulfoxide was added to 0.125 g FW (FW and incubated for 15 min in complete darkness). The supernatant was then placed into a 2.5-mL cuvette for spectrophotometric analysis (Genesys 10 UV). No further dilution was necessary. Light absorbance was recorded at wavelengths of 480, 582, 631 and 665 nm once completeness of extraction was determined (white samples).

Pigment concentration was quantified using equations from Seely et al. (1972):

$$\text{chl } a = \mathrm{A}_{665}/72.8; \qquad (1)$$

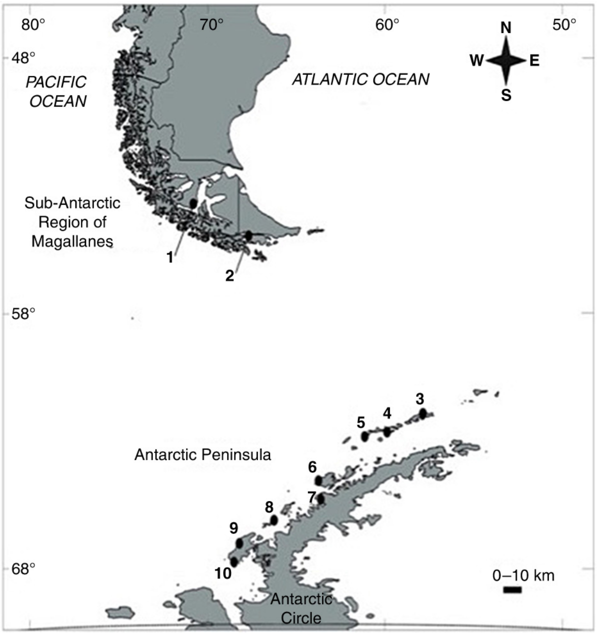

Fig. 1 Study sites sampled for *Desmarestia* species from which photosynthetic pigments chl *a* chl *c* and Fucox were extracted. Shown are the sites in the sub-Antarctic ecoregion: (1) Saint Ana Point (Brunswick Peninsula); (2) Paula Bay (Beagle Channel) and the study sites sampled in the Antarctic Peninsula; (3) Fildes Bay (Fildes); (4) Hanna Point (Hanna); (5) Prat Point (Prat); (6) Deception Island (Deception); (7) Spring Point (Spring); (8) Argentine Island (Argentine); (9) Rothera Base (Rothera); and (10) Carvajal Base (Carvajal).

$$\text{chl } c = (\mathrm{A}_{632} + \mathrm{A}_{582} - 0.297\mathrm{A}_{665})/61.8; \qquad (2)$$

$$\mathit{Fucox} = (\mathrm{A}_{480} - 0.772\ (\mathrm{A}_{631} + \mathrm{A}_{582} - 0.297\mathrm{A}_{665}) - 0.049\mathrm{A}_{665})/130 \qquad (3)$$

Data analysis

Pigment concentrations were compared among six species ($N = 7$ per species) between sub-Antarctic and Antarctic sites using the Kruskal–Wallis non-parametric test because data were not normally distributed. All conclusions were based on a 95% confidence level ($P = 0.05$). In addition, we calculated pigment ratios for species of the sub-Antarctic region and the Antarctic Peninsula and adjacent islands. All statistical analyses were carried out using the software package STATISTICA, version 7.1 (2004).

Results

Study sites

The sub-Antarctic sites showed lower average salinity and PAR light (32.35 psu and 345.5 µE/m^{2}s, respectively) but generally showed higher average temperature and dissolved oxygen (8.4°C and 12.8 mg/L, respectively) than the sites along the Antarctic Peninsula (33.4 psu, 811.2 µE/m^{2}s, 1.7 °C and 9.6 mg/L; Table 1). Average depth and habitat substrate types where *Desmarestia* specimen could be collected from for this study remained fairly constant variables across sites in both regions (Table 1).

Spatial and interspecific differences

Overall, higher average concentrations of chl *a*, chl *c* and Fucox were observed in *Desmarestia* species from Antarctic sites compared with sub-Antarctic sites (except *D. ligulata* subsp. *muelleri*; Fig. 2a). Among the sub-Antarctic species of *Desmarestia*, the highest chl *a* concentration was measured in *D. confervoides* from Paula Bay (Beagle Channel, Cape Horn Province) and the highest Fucox concentration in *D. ligulata* subsp. *muelleri* (lowest chl *a*) from the Strait of Magellan (Fig. 2a). Chl *a* concentration differed significantly between *D. ligulata* subsp. *ligulata* f. *distans* and Antarctic *D. menziesii* ($P = 0.001$; Fig. 2a). The chl *c* content of sub-Antarctic *D. confervoides* was significantly different from all *Desmarestia* species tested (all $P < 0.002$; Fig. 2a). Statistically, Fucox was most variable between the sub-Antarctic species ($P = 0.009$; Fig. 2a).

The ratio of chl *c*/chl *a* was similar in the sub-Antarctic species *D. confervoides* (1.68), *D. ligulata* subsp. *ligulata* f. *distans* (2.09) and *D. ligulata* subsp. *muelleri* (1.61; Fig. 2b). Large differences in the ratio of Fucox/chl *a* were found between *D. ligulata* subsp. *muelleri*, which exhibited an increased proportion of Fucox (5.41 in specimen from Paula Bay, Beagle Channel, Cape Horn; Fig. 2b), and all *Desmarestia* species tested. The data show similar pigment concentrations and ratios among the Antarctic Desmarestiales and overall fairly lower than in sub-Antarctic species (all between 0.31 and 0.38; Fig. 2b).

Interspecific differences along the Antarctic Peninsula: *D. antarctica* and *D. menziesii.*

The higher concentrations of chl *a* (0.45 ± 0.17 mg.g^{-1} FW) and chl *c* (0.20 ± 0.08 mg.g^{-1} FW) were generally found in *D. menziesii.* But we measured nearly identical concentrations of Fucox in both, *D. menziesii* and *D. antarctica* (Fig. 3a, b).

No clear latitudinal effect was observed for chl *a* concentration in *D. menziesii* along the Antarctic Peninsula (Fildes to Carvajal; Table 1, Fig. 3a). High concentration of chl *a* in *D. menziesii* was recorded in Deception, followed by Rothera and Carvajal (0.63 ± 0.04, 0.64 ± 0.03 and 0.63 ± 0.05 mg·g^{-1} FW, respectively), especially at the lowest temperature and salinity sites, near the Antarctic Circle (Table 1, Fig. 3a). A decreasing trend in

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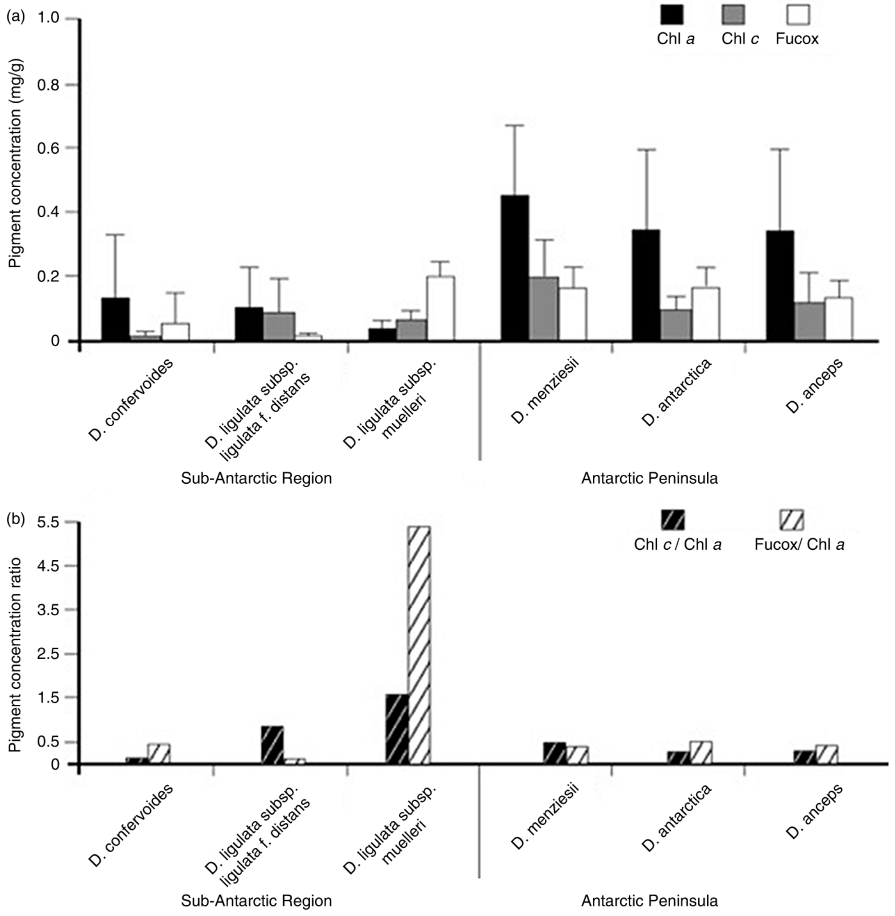

Fig. 2 (a) Mean ± SD pigment concentration ($N = 7$ per species) of chl *a*, chl *c* and Fucox and (b) ratios of mean pigment concentration ($N = 7$) of chl *c*/chl *a* and of Fucox/chl *a* in species of the genus *Desmarestia* from the sub-Antarctic region of Chile and the Chilean Antarctic Peninsula.

pigment concentration with increasing latitude was observed from Deception to Spring and Argentine sites. Chl *a*, chl *c* and Fucox in *D. menziesii* at Fildes, Spring and Argentine, with similar abiotic features (Table 1), ranged in similar, and lower, concentrations (all between 0.18 and 0.30 ± 0.03 mg·g^{-1} FW; Fig. 3a) than sites with variable PAR, temperature, salinity or substrate type (Table 1).

In *D. antarctica,* chl *a* concentration varied markedly among sites on the Antarctic Peninsula, the highest chl *a* concentrations were recorded in Deception (0.56 ± 0.2 mg·g^{-1} FW) and Carvajal (0.56 ± 0.07 mg·g^{-1} FW; Fig. 3c, d). Chl *c* concentration in *D. antarctica* decreased towards lower latitudes, from the highest values found at Deception (0.15 ± 0.09 mg·g^{-1} FW) to almost half of the concentration in samples from Fildes Bay. Fucox concentrations barely changed along the latitudinal gradient, between Deception and Spring (Fig. 3b) in spite of different environmental features (Table 1).

We identified overall higher ratios of chl *c*/chl *a* in *D. menziesii* than in *D. antarctica*, and overall higher ratios of Fucox/chl *a* in *D. antarctica* than in *D. menziesii* considering all locations along the Antarctic Peninsula (Fig. 3c, d). Among samples of *D. menziesii*, the highest chl *c*/chl *a* ratio was registered in Fildes (0.83), the lower latitude site, and the highest Fucox/chl *a* ratio was registered in Argentine (Fig. 3c). Samples of *D. antarctica* from locations along the Antarctic latitudinal gradient, showed low chl *c*/chl *a* ratio (Fig. 3d). The Fucox/chl *a* ratios in *D. antarctica* from Fildes (1.23) and Spring (1.14) were nearly triple (and double in Spring Point) that of *D. menziesii* (all sites; Fig. 3c, d).

Discussion

We analysed intraspecific and interspecific differences in pigment composition in sub-Antarctic and Antarctic samples of the genus *Desmarestia*. In the six species studied,

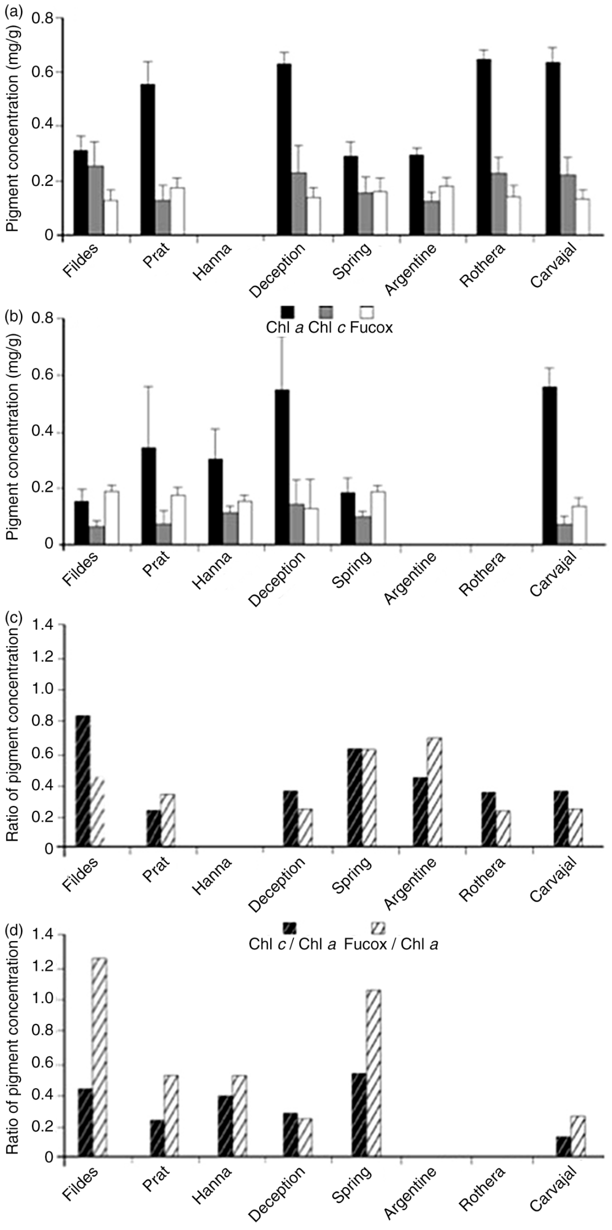

Fig. 3 Pigment concentration of (a) *Desmarestia menziesii* and (b) *D. antarctica* along a latitudinal gradient in the Antarctic Peninsula. Shown are the means ± SD ($N = 7$) concentration of chl *a*, chl *c* and Fucox, and mean concentration ratios of chl *c*/chl *a* and Fucox/chl *a* in (c) *D. menziesii* and in (d) *D. antarctica* from study sites along the Antarctic Peninsula's latitudinal gradient ($N = 7$).

we found the lowest concentrations of chl *a*, chl *c* and Fucox in the species from sub-Antarctic sites, versus the higher pigment concentrations in species along the Antarctic Peninsula (Table 1; Fig. 3), that is, increasing pigment composition towards the prevailing radiation climate. Though we registered differences between sites, we expected to see a gradient of photosynthetic pigment concentration reflecting the latitudinal gradient along the Antarctic Peninsula. We did not see this pigment gradient from our results (Fig. 3). Such a gradient may have suggested the presence of more accessory pigments in subtidal specimen as a possible strategy to optimize photosynthetic efficiency in regions with shorter light exposure (Gómez et al. 1997). Nevertheless, we saw an important tendency for higher chlorophyll concentrations at our two sites closest to the polar circle (Carvajal and Rothera) and the high-latitude site Deception, especially with *D. menziesii* (*D. antarctica* not collected in Rothera). Several biotic and abiotic factors, such as temperature, salinity, nutrients (Ramus 1978; Dhargalkar 2004; Nygård & Dring 2008) and thalli morphology (Peckol & Ramus 1988; Johansson & Snoeijs 2002), may also influence efficiency of light absorption and geographical distribution of macroalgae, survival, growth rates and reproductive success (Van den Hoek 1982; Breeman 1988) at both sub-Antarctic and Antarctic sites.

At lower temperature (usually higher latitude), high rates of photosynthesis are observed among terrestrial and aquatic plants and usually relate to an increased ratio of chl *a* to *b* (e.g., Eggert et al. 2006). Similar photosynthetic adaptations are most likely in macroalgae at high latitudes, such as those endemic species of the Antarctic Peninsula. Although the depth of light dispersion influences photosynthetic pigment composition, our samples of *Desmarestia* species were all collected in the ca. 5 m depth range in sub-Antarctica and Antarctica. It is unlikely that depth was an influential factor on the observed pigment differences. But, the variation in pigment composition among sites on the Antarctic Peninsula may be influenced by the seasonal variation in light, related in turn to variation in temperature, inducing variable pigment production and metabolic rate (e.g., Barko & Smart 1981; Aguilera et al. 2002). Similarly, seasonal sea-ice and snow coverage (Zacher et al. 2009), influencing salinity and nutrients, may also affect the physiology of photosynthesis and algal pigment content (e.g., Nygård & Dring 2008).

Desmarestia's pigment concentration may vary under different salinities or according to life history stage (Gómez & Wiencke 1996). Salinity changes affect cellular structures responsible for the synthesis and metabolism of proteins, affecting the life cycle and pigment concentration of some brown algae (Nygård & Dring 2008) and are likely to affect Antarctic species of *Desmarestia*. Nutrients also influence photosynthesis and growth rate. For example, cultivation of *Fucus vesiculosus* from the Baltic Sea (5 psu) showed higher photosynthetic activity (as electron transfer rate) and relative growth rate at low salinities (< 10 psu) than *F. vesiculosus* from the Irish Sea (35 psu), which decreased sharply in salinities below 20 psu

(Nygård & Dring 2008). Fucus specimens from both Baltic (5 psu) and Irish (20 psu) sites under high-nutrient conditions performed better at low salinities than those grown in low-nutrient cultures (Nygård & Dring 2008). Salinity may therefore be a stronger influence on differences in photosynthesis (and growth) between specimens from two geographic regions or populations, followed by differences in nutrient concentrations. A marked coastal isocline is more characteristic of Antarctic than of sub-Antarctic waters (Palma et al. 2008) and this might explain the overall lower pigment concentration and ratios in *Desmarestia* from sub-Antarctic sites than in those from Antarctica. An increase in global temperatures, with its consequent increase in glacial inflows, reduced salinity and increased water turbidity, may alter depth distribution patterns—and therefore productivity—of macroalgal communities, especially in high-latitude regions.

Though salinity barely differed between sites in both study regions, macroalgal pigment composition and concentration may also vary according to life history stage and thallus morphology (Gómez et al. 1997; Wiencke, Clayton et al. 2006). Early stages of *D. menziesii* would be better adapted to low light intensities than adult stages because they have more pigment composition per unit of biomass and therefore more investment in light-harvesting mechanisms (Gómez 2001). Alternatively, the *Desmarestia* species we examined have filamentous and laminar thalli, which directly affect the efficiency of light absorption (Ramus 1978; Peckol & Ramus 1988; Johansson & Snoeijs 2002). Thinner species have increased photosynthetic tissue per unit biomass. In *D. menziesii*, the content of chl *a*, *c* and Fucox in cultured samples increased with thallus biomass (Gómez & Wiencke 1997). The pigment composition of *D. confervoides*, of cylindrical and branched thalli morphology, showed a photosynthetic capacity between that of fleshy and laminar thalli with few cell layers (Rautenberger et al. 2009). This morphology is typical of sub-Antarctic species. Therefore, the greatest concentration of Fucox in *D. ligulata* subsp. *muelleri* (and *D. antarctica*, similar morphology) may be due to the laminar thallus morphology potentially influencing pigment concentrations (Eggert et al. 2006; Navarro et al. 2009) in these sub-Antarctic algae.

In the sub-Antarctic species, no clear pattern in pigment composition was observed from Saint Ana Point to Paula Bay near Cape Horn (Drake Passage; Fig. 1). The sub-Antarctic marine habitats are exposed to the unique confluence of three ocean influences (Reid 1989) where heavy precipitation, for instance, may set a subtle but important difference among study regions (Table 1), in addition to fluvial run off often rare in sites of the Antarctic Peninsula. This may explain the lower water salinity and higher temperatures registered in general in the physico-chemically heterogeneous sub-Antarctic environment. The greater variation in, and generally lower, pigment concentration among the sub-Antarctic *Desmarestiales* studied may result from low ice or cloud cover, decreased water turbidity from glacial run off, longer daylength in winter or large heterogeneity in the physico-chemical environment (e.g., the advance and retreat of ice [Silva & Calvete 2002]).

We found differences in pigment concentration, especially in chl *a*, between our study sites along the Antarctic Peninsula (Fildes, Prat, Deception, Spring, Argentine, Rothera and Carvajal), although the concentrations of Fucox barely changed among sites. This might be explained by the fact that accessory pigments (carotenoids) are generally less sensitive to severe environments compared with chl *a* (Häder & Häder 1989). Antarctic macroalgae may be better acclimated than other algae to withstand environmental extremes (irradiance, photoperiod, temperature, salinity, nutrients) that affect the photosynthetic efficiency and pigment composition in high latitudes (Gómez et al. 1997; Gómez 2001; Wiencke, Roleda et al. 2006).

Though we did not measure directly all possible abiotic conditions (cloud cover, transient ice), in other studies, reduced availability of PAR due to increased water turbidity from glacial influence and depth in coastal Antarctica led to decreased macroalgal vertical distribution, photosynthetic parameters (Rautenberger et al. 2013) and metabolic carbon balance (Deregibus et al. 2015). Similar works reveal that the duration of daily exposure, rather than the intensity of light, is most significant for macroalgal productivity and photosynthetic efficiency in coastal areas (Gómez et al. 1997; Zacher et al. 2009). That is, the increased pigment concentration in Antarctic algae during the summer may be a strategy to increase light-harvesting efficiency in an environment with significantly less annual solar radiation than that in temperate to tropical regions (Ramus 1981; Kirst & Wiencke 1995; Wiencke, Roleda et al. 2006).

In contrast, lower pigment content could protect individuals in regions (e.g., sub-Antarctic) with less-intense light regime (though available over longer time, that is, months per year, daylength in winter) than the short-and-intense Antarctic light regime in the summer (e.g., Gómez et al. 1997; Gómez 2001). Similar patterns have been found in a number of seaweeds from a high Arctic site (Aguilera et al. 2002). Samples were only collected in summer and therefore we were unable to test this potential strategy. In addition, photoperiod is suggested to influence the concentration of accessory pigments in Antarctic waters to a greater degree than it influences chl *a* (Yokoya et al. 2007). But, under field conditions, the effects of photoperiod and irradiance are difficult to disentangle, and thus further studies under controlled laboratory conditions are recommended. It is likely that changes occur in pigment composition of the photosynthetic antenna in sub-Antarctic *Desmarestia* (e.g., decrease in chl *a* with increased light availability in summer; our unpubl. data), but its physiological response must be further studied.

In conclusion, despite the environmental extremes of polar waters, macroalgae show physiological adaptations (Wiencke 1990). These adaptations can be seen in the photosynthetic apparatus and pigment composition (Kirst & Wiencke 1995). Amid the cumulative global and environmental changes, including increases in average temperatures—and consequent changes in salinity, light intensity and availability—there is a growing need for basic research to guide applied studies (e.g., biotechnology) using algae and their mechanisms of adaptation, survival and irradiance protection as model machinery.

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