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Photophysiology of the first reported bleached crustose coralline alga, *Clathromorphum* sp. (Hapalidiales, Rhodophyta), from Antarctica

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Abstract

During a 2019 Chilean Antarctic Scientific Expedition (ECA 55) studying crustose coralline algae (CCA) diversity on the Antarctic Peninsula, bleaching of these algae was observed for the first time in this region. Here, we present initial findings on the physiological state of bleached and normally pigmented CCA (*Clathromorphum* sp.) assessed using chlorophyll-*a* fluorescence induction pulse amplitude modulation. The study site experienced high light exposure and salinity in the water column. Our analyses found that bleached CCA have relatively healthy photophysiology responses but lower photosynthetic efficiency, which could be associated with the low salinities recorded in the study area. However, seasonal monitoring and mesocosm experiments across the southern polar latitudes are urgently required to confirm this hypothesis.

Key words: Antarctic Peninsula, irradiance, photosynthetic performance, *psb*A, *rbc*L, salinity

Introduction

Crustose coralline algae (CCA), calcifying multicellular red seaweeds, play critical ecological roles in marine environments, such as being one of the builders of coral reefs and providing habitat and settlement cues for larval and juvenile stages of invertebrates (Cornwall *et al.* 2019, Tâmega & Figueiredo 2019). CCA occur globally from the tropics to the cold waters of the polar regions (Nelson 2009). However, despite progress in describing their diversity and taxonomy (Sciuto *et al.* 2021), ecological knowledge of this group remains limited in polar latitudes, particularly in the Southern Hemisphere, including Antarctica.

The Antarctic region and the Southern Ocean, home to pristine ecosystems and unique biota, are pivotal to the stability of the global climate because of their ability to take up heat and CO_2 as well as providing important climate feedbacks through their influence on albedo and atmospheric and oceanic circulation (Jones *et al.* 2016, Convey & Peck 2019). Warming is a significant issue in this region, not least with the record highest air temperature being recorded on the continent in 2020 (18.3°C on 6 February 2020 at Argentina's Esperanza research station; World Meteorological Organization 2021). Warming also melts more land-based snow and ice, increasing freshwater runoff and causing localized lowered intertidal, subtidal and shallow water salinity (Janecki *et al.* 2010).

CCA are particularly sensitive to climate change, especially those inhabiting the Southern Ocean, due to the potential decline in their calcification rates resulting from decreased pH and carbonate ion (CO_3^{2-}) concentration as more CO_2 dissolves into ocean surface waters (Hofmann & Bischof 2014, McCoy & Kamenos 2015, Johnson *et al.* 2019, Sciuto *et al.* 2021). The photosynthetic performance of Antarctic intertidal CCA is yet to be investigated, as are the physiological traits that allow them to survive intertidal environmental conditions.

During a 2019 Antarctic expedition studying CCA diversity on the Antarctic Peninsula, bleaching of these algae was observed for the first time in this region. Such bleaching - the loss of pigmentation in algae - has been widely linked to thermal-stress events associated with climate change in tropical and subtropical regions (Martone *et al.* 2010, Cornwall *et al.* 2019, Montes-Herrera *et al.* 2024). Experiments on coralline algae have revealed a variety of causes for bleaching due to the single or combined effects of multiple environmental stressors, including water temperature change

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(Martone *et al.* 2010), acidification (Anthony *et al.* 2008), high irradiance (Dring *et al.* 1996, Martone *et al.* 2010), canopy and epiphyte loss (Figueiredo *et al.* 2000, Irving *et al.* 2005) and desiccation and salinity extremes (Sotka *et al.* 2018). Biological factors such as pathogen infection (Case *et al.* 2011) or changes in surface bacterial assemblages (Campbell *et al.* 2011) are other reported causes of bleaching events. Although the diversity in outcomes among different experimental studies, with both positive and negative physiological responses, blurs predictions of climate change impacts, this might be a result of species-specific differences (Chan *et al.* 2020, Sordo *et al.* 2020).

Over recent decades, West Antarctica and the Antarctic Peninsula have lost ice mass rapidly, three to four times more than the rest of Antarctica combined (Convey & Peck 2019). Therefore, it is relevant to study how photophysiology varies between CCA individuals undergoing different responses (bleaching phenotype) under the same environmental conditions, especially in the context of climate change and the development of future strategies for conservation in Antarctica led by Parties to the Antarctic Treaty.

Here, we present initial findings on the physiological state (photosynthetic performance) of bleached and non-bleached CCA assessed using chlorophyll-*a* fluorescence induction measured using pulse amplitude modulation (PAM) fluorometry. This study contributes to our understanding of the physiological tolerance of coralline algae that is currently lacking, especially in extreme environments such as the polar regions.

Materials and methods

CCA bleaching was observed close to the Chilean Yelcho research station on Doumer Island in a protected bay composed of rocky platforms and surrounded by glaciers, adjacent to the Peltier Channel, western Antarctic Peninsula (64°52'33"S, 63°33'46"W; Fig. 1a–c), during the 2018/2019 summer (21 February 2019). The study site is characterized by the presence of hard substrate (pebbles, larger stones, bedrock) and is protected from large waves and swells. Seven specimens each of bleached (white) and normally coloured (pale violet-red) CCA (Fig. 1d,e) were randomly collected under permit (Special Permits 198/2019 and 200/2019 issued to Universidad de Magallanes by the Instituto Antártico Chileno - INACH) from the intertidal zone. These were used to perform identification and compare their photosynthetic performances. Sampling took place around solar noon on a sunny day. Additionally, a quadrat survey was performed to analyse the bleached CCA percentage cover. Ten quadrats of 50 × 50 cm were selected randomly in the study area.

Identification of the collected CCA was performed using specialist literature (Mendoza & Cabioch 1985, Hommersand *et al.* 2009), and phylogenetic analyses were completed using standard markers from the plastid genome (*psb*A and *rbc*L). Molecular procedures were performed as described by Calderon *et al.* (2021). Primer pairs used for amplification and sequencing were F1- R2 (Yoon *et al.* 2002) for *psb*A and F57- 897cR and F645-R1150 (Freshwater & Rueness 1994, Lin *et al.* 2002, Torrano-Silva *et al.* 2014) for *rbc*L. In total, 13 new sequences (*psb*A = 6; *rbc*L = 7) were generated and have been deposited in GenBank (www.ncbi.nlm.nih.gov/genbank/; Table S1). Representative material has been deposited in the herbarium of Criptógamas Subantárticas (LEMAS) del Laboratorio de Ecosistemas Marinos Antárticos y Sub-antárticos of the Universidad de Magallanes, Punta Arenas, Chile (UMAG).

Photosynthetic activity was measured *in situ* on crusts using a pulse-amplitude-modulated chlorophyll fluorometer 'MINI-PAM-II' (Walz GmbH, Germany). Photosynthetic performance was measured *in vivo* after 15 min of dark adaption, and rapid light curves (RLC) were recorded using an actinic light of 0–2950 µmol photons m^{-2} s^{-1} (Marambio *et al.* 2023). The standard photosynthetic parameters as relative maximum electron transport rate ($rETR_{max}$), electron transport efficiency (α, initial linear slope), light saturation point of photosynthesis (E_k) and quantum yield of photosystem II (F_v/F_m) were estimated for both bleached and coloured CCA following the procedures described by Wilson *et al.* (2004) and Méndez *et al.* (2018). Studies of photosynthetic performance commonly use a minimum of two to three measurements per group (see Gómez *et al.* 1997, Payri *et al.* 2001, Chisholm 2003). Here, the photosynthetic parameters $rETR_{max}$, α, E_k and the ratio of F_v/F_m were measured on three individuals each of bleached and coloured CCA. Temperature (°C) and salinity (psu) were measured using an SBE 19plus v2 CTD device (Sea-Bird Scientific, USA) in the water column, and pH was measured using a portable pH meter ProfiLine pH 3110 (WTW, Germany). Radiation data were obtained from WeatherOnline Ltd - Meteorological Services (www.weatheronline.co.uk) for Palmer Station (64°46'S, 64°03'W), 26 km north-west of our collection point. Photosynthetically active radiation (PAR) was calculated using the *R* package 'bigleaf' to convert radiation (W m^{-2}) to photosynthetic photon flux density (PPFD).

Results

We report the presence of bleached CCA for the first time in the Antarctic Peninsula region. The specimens collected were consistent with the morphological description of the genus *Clathromorphum* (Hapalidiales, Rhodophyta). The phylogenetic reconstruction based on *psb*A and *rbc*L sequences (Fig. S2) did not group our specimens with the generitype *Clathromorphum compactum*, rather clustering them in an independent lineage within the order Hapalidiales (Figs S1 & S2). Since the identification of coralline algae is notoriously difficult, further studies are required to confirm the taxonomic position of these specimens, hereafter referred to as *Clathromorphum* sp.

Approximately 20% of intertidal CCA were bleached. Most of the instances of bleached CCA occurred at apparently random points on extensive solid rock surfaces and hemispherical boulders (~15–20 cm radius), the bleached area covering up to 70% of such boulders (Fig. 1d). Bleaching initiated at the periphery of the encrusting algae, advancing irregularly in the undulating margins (Fig. 1e). The surrounding red alga *Palmaria decipiens* also showed bleached regions at the margins and tips of its thalli (Fig. 1d). *In situ* environmental variables recorded at the study site included pH 8.1, temperatures between +4.5°C (at 0 m) and +1.7°C (at 25 m depth; Fig. 2a) and a gradient of salinity in the water column ranging from 0.15 (at 0 m) to 32.39 (at 25 m depth) psu (Fig. 2b), with the presence of a halocline between 10 and 12 m (3.12–16.3 psu; Table S2). PAR varied between 492.7 and 740.4 µmol photons m^{-2} s^{-1} (Table S3).

Despite the limited number of specimens included in the photophysiological analysis, some interesting observations were apparent.

For instance, similar ranges of measurement were recorded for $rETR_{max}$, α and F_v/F_m in both CCA. $rETR_{max}$ varied from 3.45 to 23.80 relative units (r.u.) in coloured CCA and from 15.48 to 16.48 r.u. in bleached CCA, while α ranged from 0.05 to 0.21 (µmol photons m^{-2} $s^{-1})^{-1}$ in coloured CCA and from 0.08 to 0.11 (µmol photons m^{-2} $s^{-1})^{-1}$ in bleached CCA. Furthermore, F_v/F_m varied from 0.28 to 0.38 and from 0.11 to 0.39 in coloured

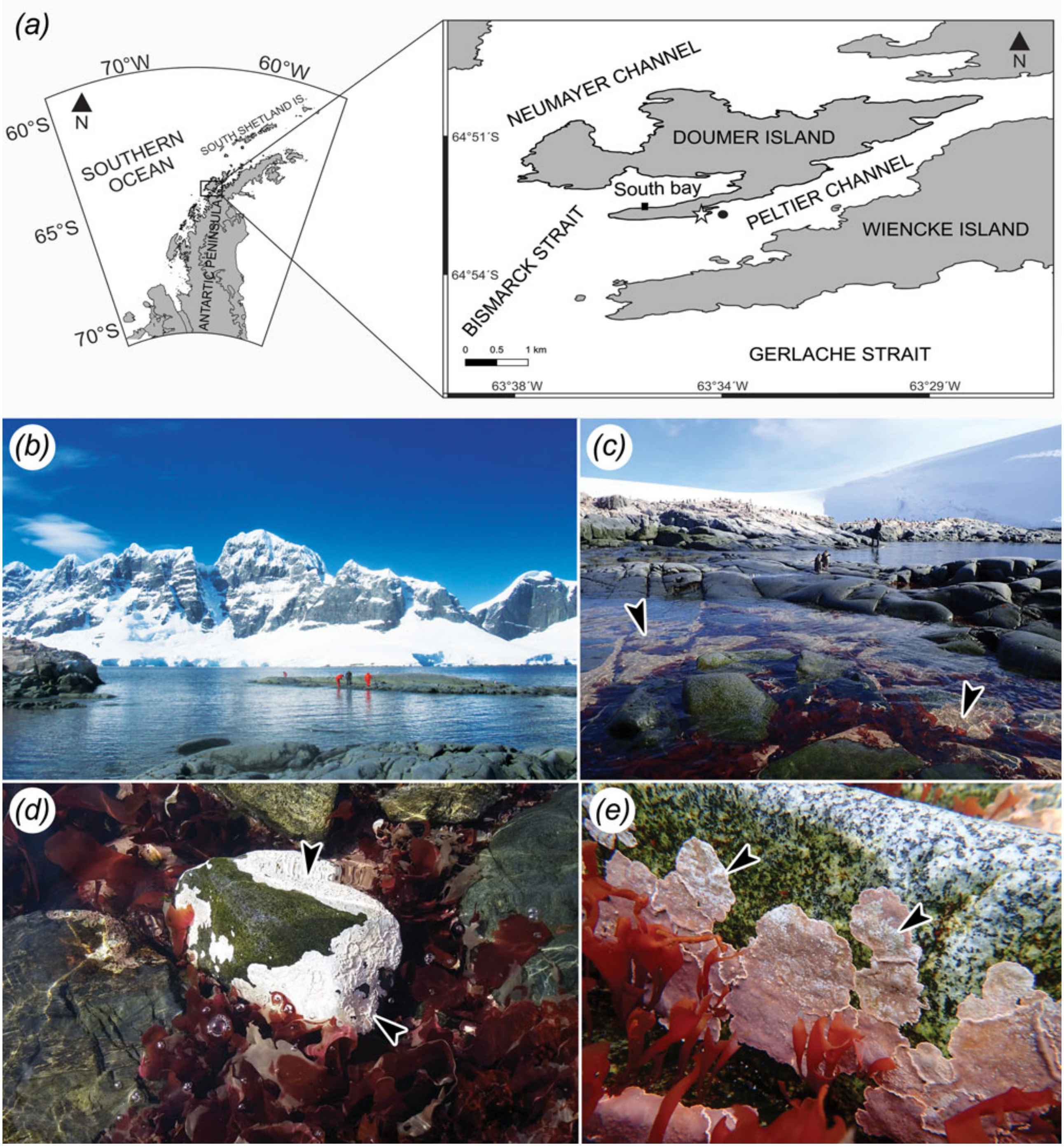

Figure 1. a. Map of the western Antarctic Peninsula coastline showing the study site (white star) and point of environmental parameter measurements (black circle), both near the Chilean Yelcho research station (black square). **b.** The landscape of the collection area. **c.** Beds of crustose coralline algae (arrowheads) in the intertidal zone. **d.** Stone covered by bleached *Clathromorphum* sp. (arrowheads) surrounded by the red alga *Palmaria decipiens*, also showing some bleaching spots. **e.** Close-up of crustose coralline algae showing the initial stages of bleaching in the margins of the algae (arrowheads).

and bleached CCA, respectively. Conversely, E_k ranged from 69.87 to 115.99 µmol photons m^{-2} s^{-1} and from 146.08 to 209.36 µmol photons m^{-2} s^{-1} in coloured and bleached CCA, respectively (Fig. 2c–f & Table I).

Discussion

Photosynthetic performance of the intertidal calcareous coralline algae *Clathromorphum* sp. from Antarctica has not been explored previously. The genus *Clathromorphum* is very common along the Antarctic Peninsula, where it can dominate communities in intertidal pools and the subtidal seascape (Mendoza & Cabioch 1985, Hommersand *et al.* 2009). It typically occurs low on the shore (< 0.3 m tide height) and in mid-intertidal tidepools, where exposure to light stress and desiccation is likely to be reduced during low tide. Here, it was not possible to achieve species-level identification since three species of the genus *Clathromorphum* - *C. annulatum*, *C. lemoineanum* and

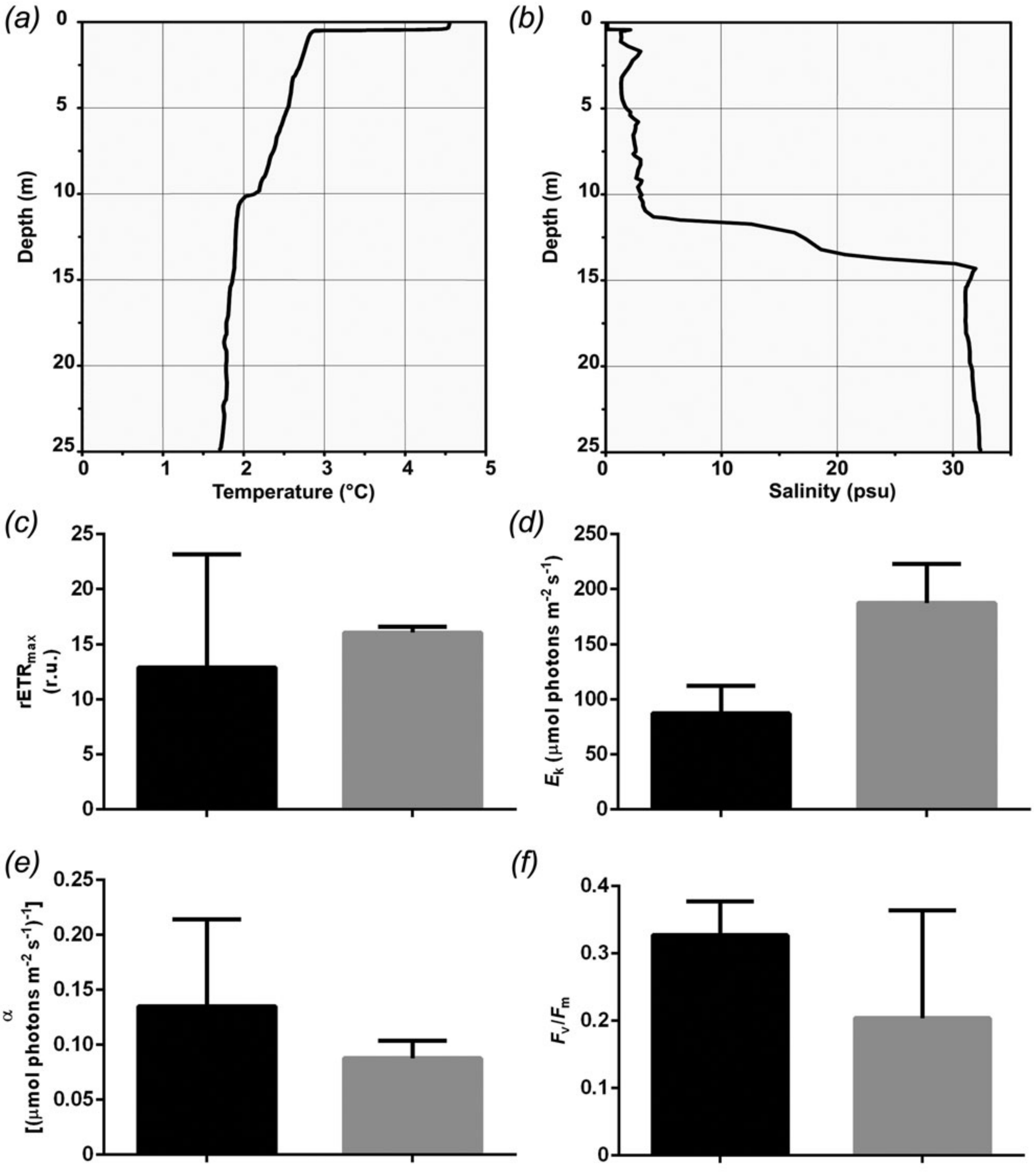

Figure 2. Variation in **a.** temperature and **b.** salinity in the water column. Photosynthetic parameters of healthy (black bars) and bleached (grey bars) crustose coralline algae calculated from chlorophyll-*a* fluorescence measurements for **c.** relative maximum electron transport rate, ($rETR_{max}$), **d.** light saturation point of photosynthesis (E_k), **e.** electron transport efficiency (α) and **f.** the quantum yield of photosystem II (F_v/F_m). r.u. = relative units.

C. obtectulum - have been reported in West Antarctica, and descriptions suggest that they share habitat and ecological features (Mendoza & Cabioch 1985, Hommersand *et al.* 2009). Thus, further taxonomic studies are required to confirm the phylogenic position of our specimens.

Our results derived from RLC measures, such as $rETR_{max}$ (r.u.), E_k (μmol photons m^{-2} s^{-1}) and α ((μmol photons m^{-2} $s^{-1})^{-1}$), of both coloured (3.45–23.80 r.u.; 69.87–115.99 μmol photons m^{-2} s^{-1}; 0.05–0.21 (μmol photons m^{-2} $s^{-1})^{-1}$) and bleached CCA (15.48–16.48 r.u.; 146.08–209.36 μmol photons m^{-2} s^{-1}; 0.08–0.11 (μmol photons m^{-2} $s^{-1})^{-1}$) were consistent with values reported in intertidal uncalcified red algae from Antarctica, such as *Pyropia endiviifolia* (10.82 ± 1.76 r.u.; 96.61 ± 26.13 μmol photons m^{-2} s^{-1}; 0.11 ± 0.02 (μmol photons m^{-2} $s^{-1})^{-1}$), *Palmaria decipiens*

Table I. Photosynthetic parameters of the crustose coralline algae (CCA) *Clathromorphum* sp. (bleached and coloured).

Parameters	No.	Coloured CCA	Bleached CCA
rETR$_{max}$ (relative units)	1	23.80	16.48
	2	3.45	15.48
	3	11.55	16.32
	Mean	12.93	16.09
	SD	10.24	0.54
α ((µmol photons m^{-2} s^{-1})$^{-1}$)	1	0.21	0.08
	2	0.05	0.11
	3	0.15	0.08
	Mean	0.14	0.09
	SD	0.08	0.02
E_k (µmol photons m^{-2} s^{-1})	1	115.99	206.51
	2	69.87	146.08
	3	76.58	209.36
	Mean	87.48	187.32
	SD	24.92	35.74
F_v/F_m	1	0.32	0.12
	2	0.38	0.11
	3	0.28	0.39
	Mean	0.33	0.20
	SD	0.05	0.16

α = electron transport efficiency; E_k = light saturation point of photosynthesis; F_v/F_m = quantum yield of photosystem II; rETR$_{max}$ = relative maximum electron transport rate.

(13.36 ± 3.97 r.u.; 78.58 ± 17.66 µmol photons m^{-2} s^{-1}; 0.17 ± 0.05 (µmol photons m^{-2} s^{-1})$^{-1}$) and *Iridaea cordata* (18.61 ± 2.08 r.u.; 101.76 ± 15.17 µmol photons m^{-2} s^{-1}; 0.18 ± 0.04 (µmol photons m^{-2} s^{-1})$^{-1}$; Gómez *et al.* 2019). The photosynthesis-irradiance (P-E) curve parameters (i.e. rETR$_{max}$ and E_k), which vary in relation with depth (Gómez *et al.* 2019), are overall higher in eulittoral species than those collected from the subtidal zone and are not constrained by algal taxonomy (Huovinen & Gómez 2013). Additionally, the light requirements for photosynthesis (E_k) measured here in bleached CCA (E_k = 146.08–209.36 µmol photons m^{-2} s^{-1}) were the highest values recorded for a shallow subtidal red alga in Antarctica, followed by *Curdiea racovitzae* (E_k = 92.73 ± 8.22 µmol photons m^{-2} s^{-1}) and *I. cordata* (E_k = 121.26 ± 27.53 µmol photons m^{-2} s^{-1}) and *Pantoneura plocamioides* (E_k = 149.39 ± 30.06 µmol photons m^{-2} s^{-1}; Gómez *et al.* 2019), further supporting the notion of their strong resilience to exposure to high levels of PAR (Payri *et al.* 2001, Wiencke *et al.* 2007). Polar algae from the upper sublittoral or eulittoral typically show high values of saturation points for photosynthesis (E_k > 50 µmol photons m^{-2} s^{-1}; Weykam *et al.* 1996, Gómez *et al.* 1997, Payri *et al.* 2001).

Photosynthetic studies of CCA in polar regions have focused to date on subtidal samples, complicating the comparison of parameters (Kühl *et al.* 2001, Roberts *et al.* 2002, Schwarz *et al.* 2005, Schoenrock *et al.* 2018). Despite this, the measured photosynthetic performance ranges (rETR$_{max}$; E_k) of both normally coloured and bleached CCA from Doumer Island were higher than those of other intertidal calcareous algae studied in temperate regions, such as *Lithothamnion glaciale* from the west coast of Scotland (3.83 ± 0.52 r.u.; 54.61 ± 5.29 µmol photons m^{-2} s^{-1}) and *Chamberlainium* sp. from Garorim Bay in South Korea (8.2 ± 0.26 r.u.; 57.1 ± 2.6 µmol photons m^{-2} s^{-1}; Burdett *et al.* 2012, Kim *et al.* 2020).

Most intertidal algal species examined in Antarctica have previously been shown to have high photosynthetic efficiency (α > 0.15 (µmol photons m^{-2} s^{-1})$^{-1}$; Gómez *et al.* 1997, Gómez & Huovinen 2011), while the quantum yield of photosystem II (PSII; F_v/F_m) for red algae is typically 0.5–0.6 (Dring *et al.* 1996, Burdett *et al.* 2012). The low values of F_v/F_m measured here in both bleached (0.043–0.363) and coloured CCA (0.277–0.377) might suggest physiological stress and inefficiency of energy transfer to the PSII reaction centres (Dring *et al.* 1996, Wilson *et al.* 2004, Schoenrock *et al.* 2018), perhaps associated with exposure to low salinities. Our observations showed a strong gradient in salinity in the water column from hyposaline conditions (1.37 psu at 0.5 m depth) to a halocline between 10 and 12 m depth (3.12–16.30 psu), so further experimental work, including increase sample size and effort, is required to explore whether a reduction in salinity has major implications for photosynthesis in Antarctic *Clathromorphum* sp., as metabolic processes that control salinity tolerance also remain poorly understood in Antarctic calcareous algae (Karsten 2012). Future *in situ* and laboratory experimental studies should also include short-term exposure to salinities close to freshwater values as well to reflect stresses associated with freshwater runoff across the shoreline from melt.

As we were not able to sample or monitor CCA over time, it was not possible to assess the duration of bleaching or recovery time (or if recovery occurred) of these bleached CCA. Thus, further studies that monitor pigment content, calcification rate and $CaCO_3$ skeleton thickness, singlet-oxygen ($^1O_2$) production and concentrations of antioxidant dimethylated sulphur compounds (dimethylsulphoniopropionate (DMSP) and dimethyl sulphoxide (DMSO)) over seasonal timescales are now required, as has been carried out in previous studies of other non-polar CCA (Latham 2008, Burdett *et al.* 2015a, 2015b, Schoenrock *et al.* 2018, Muth *et al.* 2020, Montes-Herrera *et al.* 2024).

Bleaching is often thought to be an indicator of death (Irving *et al.* 2004), although colour restoration has been observed after provision of shade, low irradiance exposure or salinity values > 30 psu (Dring *et al.* 1996, Figueiredo *et al.* 2000, Irving *et al.* 2004, Muth *et al.* 2020). However, measurements such as those reported here, confirming non-zero ETR values in bleached CCA, suggest bleaching is not necessarily associated with algal death. The study site was characterized by specific conditions (high irradiance and low salinity) that have been associated with bleaching and shifts in photosynthetic parameters of coralline algae in previous studies (Kirst 1989, Roberts *et al.* 2002, Thomas & Dieckmann 2002, Irving *et al.* 2005, Latham 2008, Burdett *et al.* 2015b, Schoenrock *et al.* 2018). Our observations highlight the importance of establishing appropriate monitoring of marine environmental variables in key locations (as proposed within the Scientific Committee on Antarctic Research (SCAR) Antarctic Near-Shore and Terrestrial Observation System (ANTOS) initiatives, www.scar.org/science/cross/antos) in order to provide data that will assist in identifying and tracking the origin and duration of marine anomalies, since the environmental conditions that could have caused the bleaching of CCA reported here could have initiated before our observations.

While bleaching has been documented in CCA at temperate and tropical latitudes (Figueiredo *et al.* 2000, Martone *et al.* 2010, Vargas-Ángel 2010, Campbell *et al.* 2011), there are no previous reports of its occurrence as a natural event in the polar regions. Subtidal video recordings (Supplemental Material) showed bleaching in almost 80% of CCA located at 8–11 m depth, where the halocline was observed. Historically, the area between Anvers Island and Adelaide Island along the coast of the western Antarctic Peninsula (64°S–67°35'S), where our observations were made, has been very poorly studied, with the existence or extent of any marine changes occurring being undocumented (Wiencke & Amsler 2012). Our initial study provides a starting point to both urgently draw attention to this bleaching event in the Antarctic Peninsula region and to improve understanding of bleaching in CCA and of its wider implications for Antarctic marine communities. It is already clear that bleached CCA have relatively healthy photophysiology responses ($\mathrm{rETR_{max}}$, E_k), but with lower photosynthetic efficiency (F_v/F_m), possibly associated with the low salinities recorded in the study area; however, seasonal monitoring of key environmental parameters and mesocosm experiments across the southern polar latitudes are urgently required to confirm this hypothesis.

A range of consequences of climatic and other environmental changes in Antarctica have been reported (e.g. biological invasions, changing sea ice, ocean acidification and also now bleaching of CCA; Anthony *et al.* 2008, Abram *et al.* 2014, Convey & Peck 2019, Siegert *et al.* 2019, 2023), threats that are placing its unique and often highly endemic biodiversity at risk, yet are still waiting for political acceptance, reaction and effective response. Notwithstanding, an important element in any future strategy is that funding agencies from the national Antarctic Treaty Parties need now to develop ambitious commitments to tackle these growing concerns by investing in research, monitoring and protection programmes across Antarctica.

CRediT authorship contribution statement. MSC, DEB, AM and PC conceived the study. MSC, DEB, AM, FM and JPR conducted fieldwork. FM and JM performed and assessed the photosynthetic analyses. JPR collected environmental parameters. MSC, DEB and PC drafted the manuscript. All authors discussed the results, contributed to revisions of the manuscript, approved the final version and agree to be held accountable for the content.

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Competing interests. The authors declare no relevant financial or non-financial interests to disclose.

Data availability. Molecular data are available on GenBank (OQ471937-OQ471949).

Statement. All data are included in the Supplemental Material. The subtidal video is deposited at https://doi.org/10.6084/m9.figshare.22177178.v1.

Supplemental material. Two supplemental figures and three supplemental tables will be found at https://doi.org/10.1017/S0954102024000361.

References

Abram, N.J., Mulvaney, R., Vimeux, F., Phipps, S.J., Turner, J. & England, M.H. 2014. Evolution of the southern annular mode during the past millennium. *Nature Climate Change*, **4**, 10.1038/nclimate2235.

Anthony, K.R.N., Kline, D.I., Diaz-Pulido, G., Dove, S. & Hoegh-Guldberg, O. 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 10.1073/pnas.0804478105.

Burdett, H.L., Hatton, A.D. & Kamenos, N.A. 2015a. Coralline algae as a globally significant pool of marine dimethylated sulfur. *Global Biogeochemical Cycles*, **29**, 10.1002/2015GB005274.

Burdett, H.L., Hatton, A.D. & Kamenos, N.A. 2015b. Effects of reduced salinity on the photosynthetic characteristics and intracellular DMSP concentrations of the red coralline alga, *Lithothamnion glaciale*. *Marine Biology*, **162**, 10.1007/s00227-015-2650-8.

Burdett, H.L., Hennige, S.J., Francis, F.T.-Y. & Kamenos, N.A. 2012. The photosynthetic characteristics of red coralline algae, determined using pulse amplitude modulation (PAM) fluorometry. *Botanica Marina*, **55**, 10.1515/bot-2012-0135.

Calderon, M.S., Bustamante, D.E., Gabrielson, P.W., Martone, P.T., Hind, K.R., Schipper, S.R. & Mansilla, A. 2021. Type specimen sequencing, multilocus analyses, and species delimitation methods recognize the cosmopolitan *Corallina berteroi* and establish the northern japanese *C. yendoi* sp. nov. (Corallinaceae, Rhodophyta). *Journal of Phycology*, **57**, 10.1111/jpy.13202.

Campbell, A.H., Harder, T., Nielsen, S., Kjelleberg, S. & Steinberg, P.D. 2011. Climate change and disease: bleaching of a chemically defended seaweed. *Global Biogeochemical Cycles*, **17**, 10.1111/j.1365-2486.2011.02456.x.

Case, R.J., Longford, S.R., Campbell, A.H., Low, A., Tujula, N. Steinberg, P.D. & Kjelleberg, S. 2011. Temperature induced bacterial virulence and bleaching disease in a chemically defended marine macroalga. *Environmental Microbiology*, **13**, 10.1111/j.1462-2920.2010.02356.x.

Chan, P.T.W., Halfar, J., Adey, W.H., Lebednik, P.A., Steneck, R., Norley, C.J.D. & Holdsworth, D.W. 2020. Recent density decline in wild-collected subarctic crustose coralline algae reveals climate change signature. *Geology*, **48**, 10.1130/G46804.1.

Chisholm, J.R.M. 2003. Primary productivity of reef-building crustose coralline algae. *Limnology and Oceanography*, **48**, 1376–1387.

Convey, P. & Peck, L.S. 2019. Antarctic environmental change and biological responses. *Science Advances*, **11**, 10.1126/sciadv.aaz0888.

Cornwall, C.E., Diaz-Pulido, G. & Comeau, S. 2019. Impacts of ocean warming on coralline algal calcification: meta-analysis, knowledge gaps, and key recommendations for future research. *Frontiers in Marine Science*, **6**, 10.3389/fmars.2019.00186.

Dring, M.J., Wagner, A., Boeskov, J. & Lüning, K. 1996. Sensitivity of intertidal and subtidal red algae to UVA and UVB radiation, as monitored by chlorophyll fluorescence measurements: influence of collection depth and season, and length of irradiation. *European Journal of Phycology*, **31**, 10.1080/09670269600651511.

Figueiredo, M.A.deO., Kain (Jones), J.M. & Norton, T.A. 2000. Responses of crustose corallines to epiphyte and canopy cover. *Journal of Phycology*, **36**, 10.1046/j.1529-8817.2000.98208.x.

Freshwater, D.W. & Rueness, J. 1994. Phylogenetic relationships of some European *Gelidium* (Gelidiales, Rhodophyta) species based upon *rbc*L nucleotide sequence analysis. *Phycologia*, **33**, 187–194.

Gómez, I. & Huovinen, P. 2011. Morpho-functional patterns and zonation of south Chilean seaweeds: the importance of photosynthetic and bio-optical traits. *Marine Ecology - Progress Series*, **422**, 10.3354/meps08937.

Gómez, I., Navarro, N.P. & Huovinen, P. 2019. Bio-optical and physiological patterns in Antarctic seaweeds: a functional trait based approach to characterize vertical zonation. *Progress in Oceanography*, **174**, 10.1016/j.pocean.2018.03.013.

Gómez, I., Weykam, G., Klöser, H. & Wiencke, C. 1997. Photosynthetic light requirements, daily carbon balance and zonation of sublittoral macroalgae from King George Island (Antarctica). *Marine Ecology - Progress Series*, **148**, 281–293.

Hofmann, L.C. & Bischof, K. 2014. Ocean acidification effects on calcifying macroalgae. *Aquatic Biology*, **22**, 10.3354/ab00581.

Hommersand, M.H., Moe, R.L., Amsler, C.D. & Fredericq, S. 2009. Notes on the systematics and biogeographical relationships of Antarctic and sub-Antarctic Rhodophyta with descriptions of four new genera and five new species. *Botanica Marina*, **52**, 10.1515/BOT.2009.081.

Huovinen, P. & Gómez, I. 2013. Photosynthetic characteristics and UV stress tolerance of Antarctic seaweeds along the depth gradient. *Polar Biology*, **36**, 10.1007/s00300-013-1351-3.

Irving, A.D., Connell, S.D. & Elsdon, T.S. 2004. Effects of kelp canopies on bleaching and photosynthetic activity of encrusting coralline algae. *Journal of Experimental Marine Biology and Ecology*, **310**, 10.1016/j.jembe.2004.03.020.

Irving, A.D., Connell, S.D., Johnston, E.L., Pile, A.J. & Gillanders, B.M. 2005. The response of encrusting coralline algae to canopy loss: an independent test of predictions on an Antarctic coast. *Marine Biology*, **147**, 10.1007/s00227-005-0007-4.

Janecki, T., Kidawa, A. & Potocka, M. 2010. The effects of temperature and salinity on vital biological functions of the Antarctic crustacean *Serolis polita*. *Polar Biology*, **33**, 10.1007/s00300-010-0779-y.

Johnson, M.D., Rodriguez Bravo, L.M., O'Connor, S.E., Varley, N.F. & Altieri, A.H. 2019. pH variability exacerbates effects of ocean acidification on a Caribbean crustose coralline alga. *Frontiers in Marine Science*, **150**, 10.3389/fmars.2019.00150.

Jones, J.M., Gille, S.T., Goosse, H., Abram, N.J., Canziani, P.O., Charman, D.J., *et al.* 2016. Assessing recent trends in high-latitude Southern Hemisphere surface climate. *Nature Climate Change*, **6**, 10.1038/NCLIMATE3103.

Karsten, U. 2012. Seaweed acclimation to salinity and desiccation stress. *In* Wiencke, C. Bischof, K., *eds*, *Seaweed biology - novel insights into ecophysiology, ecology and utilization*. Berlin: Springer-Verlag, 87–107.

Kim, J.-H., Kim, N., Moon, H., Lee, S., Jeong, S.-Y., Diaz-Pulido, G., *et al.* 2020. Global warming offsets the ecophysiological stress of ocean acidification on temperate crustose coralline algae. *Marine Ecology - Progress Series* **157**, 10.1016/j.marpolbul.2020.111324.

Kirst, G.O. 1989. Salinity tolerance of eukaryotic marine algae. *Annual Review of Plant Physiology and Plant Molecular Biology*, **40**, 21–53.

Kühl, M., Glud, R.N., Borum, J., Roberts, R. & Rysgaard, S. 2001. Photosynthetic performance of surface-associated algae below sea ice as measured with a pulse-amplitude-modulated (PAM) fluorometer and O_2 microsensors. *Marine Ecology - Progress Series*, **223**, 10.3354/meps223001.

Latham, H. 2008 Temperature stress-induced bleaching of the coralline alga *Corallina officinalis*: a role for the enzyme bromoperoxidase. *Bioscience Horizons*, **1**, 10.1093/biohorizons/hzn016.

Lin, S.M., Fredericq, S. & Hommersand, M.H. 2002. Systematics of the Delesseriaceae (Ceramiales, Rhodophyta) based on large subunit rDNA and *rbc*L sequences, including the Phycodryoideae, subfam. nov. *Journal of Phycology*, **37**, 881–899.

Marambio, J., Rodríguez, J.P., Rosenfeld, S., Méndez, F., Ojeda, J., Ocaranza, P., *et al.* 2023. New ecophysiological perspectives on the kelp *Macrocystis pyrifera*: generating a basis for sustainability in the sub-Antarctic region. *Frontiers in Marine Science*, **10**, 10.3389/fmars.2023.1222178

Martone, P.T., Alyono, M. & Stites, S. 2010. Bleaching of an intertidal coralline alga: untangling the effects of light, temperature, and desiccation. *Marine Ecology - Progress Series*, **416**, 10.3354/meps08782.

McCoy, S.J. & Kamenos, N.A. 2015. Coralline algae (Rhodophyta) in a changing world: integrating ecological, physiological, and geochemical responses to global change. *Journal of Phycology*, **51**, 10.1111/jpy.12262.

Méndez, F., Marambio, J., Ojeda, J., Rosenfeld, S., Rodríguez, J.P., Tala, F. & Mansilla, A. 2018. Variation of the photosynthetic activity and pigment composition in two morphotypes of *Durvillaea antarctica* (Phaeophyceae) in the sub-Antarctic ecoregion of Magallanes, Chile. *Journal of Applied Phycology*, **31**, 10.1007/s10811-018-1675-z.

Mendoza, M.L. & Cabioch, J. 1985. Critique et comparaison morphogénétique des genres *Clathromorphum* et Antarcticophyllum (Rhodophyta, Corallinaceae). Conséquences biogéographiques et systématiques. *Cahiers de Biologie Marine*, **26**, 251–266.

Montes-Herrera, J.C., Cimoli, E., Cummings, V.J., D'Archino, R., Nelson, W.A., Lucieer, A., & Lucieer, V. 2024. Quantifying pigment content in crustose coralline algae using hyperspectral imaging: a case study with *Tethysphytum antarcticum* (Ross Sea, Antarctica). *Journal of Phycology*, **60**, 10.1111/jpy.13449

Muth, A.F., Esbaugh, A.J. & Dunton, K.H. 2020. Physiological responses of an arctic crustose coralline alga (*Leptophytum foecundum*) to variations in salinity. *Frontiers in Plant Science*, **11**, 10.3389/fpls.2020.01272.

Nelson, W.A. 2009. Calcified macroalgae - critical to coastal ecosystems and vulnerable to change: a review. *Marine and Freshwater Research*, **60**, 10.1071/MF08335.

Payri, C.E., Maritorena, S., Bizeau, C. & Rodière, M. 2001. Photoacclimation in the tropical coralline alga *Hydrolithon onkodes* (Rhodophyta, Corallinaceae) from a French Polynesian reef. *Journal of Phycology*, **37**, 223–234.

Roberts, R.D., Kühl, M., Glud, R.N. & Rysgaard, S. 2002 Primary production of crustose coralline red algae in a high arctic fjord. *Journal of Phycology*, **38**, 10.1046/j.1529-8817.2002.01104.x.

Schoenrock, K.M., Bacquet, M., Pearce, D., Rea, B.R., Schofield, J.E., Lea, J., *et al.* 2018. Influences of salinity on the physiology and distribution of the arctic coralline algae, *Lithothamnion glaciale* (Corallinales, Rhodophyta). *Journal of Phycology*, **54**, 10.1111/jpy.12774.

Schwarz, A.-M., Hawes, I., Andrew, N., Mercer, M., Cummings, V. & Thrush, S. 2005. Primary production potential of non-geniculate coralline algae at Cape Evans, Ross Sea, Antarctica. *Marine Ecology - Progress Series*, **294**, 10.3354/meps294131.

Sciuto, K., Moschin, E., Alongi, G., Cecchetto, M., Schiaparelli, S., Caragnano, A., *et al.* 2021. *Tethysphytum antarcticum* gen. et sp. nov. (Hapalidiales, Rhodophyta), a new non-geniculate coralline alga from Terra Nova Bay (Ross Sea, Antarctica): morpho-anatomical characterization and molecular phylogeny. *European Journal of Phycology*, **56**, 10.1080/09670262.2020.1854351.

Siegert, M., Atkinson, A., Banwell, A., Brandon, M., Convey, P., Davies, B., *et al.* 2019. The Antarctic Peninsula under a 1.5°C global warming scenario. *Frontiers in Environmental Science*, **7**, 10.3389/fenvs.2019.00102.

Siegert, M., Bentley, M., Atkinson, A., Bracegirdle, T., Convey, P., Davies, B., *et al.* 2023. Antarctic extreme events. *Frontiers in Environmental Science*, **11**, 10.3389/fenvs.2023.1229283.

Sordo, L., Santos, R., Barrote, I., Freitas, C. & Silva, J. 2020. Seasonal photosynthesis, respiration, and calcification of a temperate maërl bed in southern Portugal. *Frontiers in Marine Science*, **7**, 10.3389/fmars.2020.00136.

Sotka, E., Murren, C. & Strand, A. 2018. Data describing bleaching in algae collected from Antarctica, Fiji, and California when stressed by heat, cold, or low salinity. Biological and Chemical Oceanography Data Management Office (BCO-DMO). (Version 1) Version Date 2018-08-20. Retrieved from https://www.bco-dmo.org/dataset/743763

Tâmega, F.T.S. & Figueiredo, M.A.O. 2019. Colonization, growth and productivity of crustose coralline algae in sunlit reefs in the Atlantic southernmost coral reef. *Frontiers in Marine Science*, **6**, 10.3389/fmars.2019.00081.

Thomas, D.N. & Dieckmann, G.S. 2002. Antarctic sea ice - a habitat for extremophiles. *Science*, **295**, 10.1126/science.1063391.

Torrano-Silva, B.N., Riosmena-Rodriguez, R. & Oliveira, M. C. 2014. Systematic position of *Paulsilvella* in the Lithophylloideae (Corallinaceae, Rhodophyta) confirmed by molecular data. *Phytotaxa*, **190**, 10.11646/phytotaxa.190.1.8.

Vargas-Ángel, B. 2010. Crustose coralline algal diseases in the U.S.-affiliated Pacific Islands. *Coral Reefs*, **29**, 10.1007/s00338-010-0646-x.

Weykam, G., Gómez, I., Wiencke, C., Iken, K. & Klöser, H. 1996. Photosynthetic characteristics and C:N ratios of macroalgae from King George Island (Antarctica). *Journal of Experimental Marine Biology and Ecology*, **204**, 1–22.

Wiencke, C. & Amsler, C.D. 2012. Seaweeds and their communities in polar regions. *In* Wiencke, C. & Bischof, K., *eds*, *Seaweed biology - novel insights into ecophysiology, ecology and utilization*. Berlin: Springer-Verlag, 265–291.

Wiencke, C., Clayton, M.N., Gómez, I., Iken, K., Lüder, U.H., Amsler, C.D., *et al.* 2007. Life strategy, ecophysiology and ecology of seaweeds in polar waters. *Reviews in Environmental Science and Bio/Technology*, **6**, 10.1007/s11157-006-9106-z.

Wilson, S., Blake, C., Berges, J.A. & Maggs, C.A. 2004. Environmental tolerances of free-living coralline algae (maerl): implications for European marine conservation. *Biological Conservation*, **120**, 10.1016/j.biocon.2004.03.001.

World Meteorological Organization. 2021. WMO verifies one temperature record for Antarctic continent and rejects another. Retrieved from https://public.wmo.int/en/media/press-release/wmo-verifies-one-temperature-record-antarctic-continent-and-rejects-another

Yoon, H.S., Hacket, J.D. & Bhattacharya, D. 2002. A single origin of the peredinin- and fucoxanthin-containing plastids in donoflagellates through tertiary endosymbiosis. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 11724–11729.