



New confirmed depth limit of Antarctic macroalgae: *Palmaria decipiens* found at 100 m depth in the Southern Ocean

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Abstract

Living specimens of the macroalga *Palmaria decipiens* were collected from 100 m depth, representing a new confirmed depth record, considerably exceeding the previous record of 42 m depth. Previous deeper collections (below conventional SCUBA depths) have relied on dredge/grab samples or drop camera surveys. Remote techniques cannot conclusively prove that macroalgae are living at these depths, as algae detach from shallower substrata, e.g., through ice scouring, and drift to depths below their growth limit. This, combined with a low rate of decay of macroalgae around Antarctica, requires validation that algal samples from depth have grown in situ. Estimates of macroalgal biomass, energy fluxes, and the potential energy fixation may need adjusting to consider the deeper growing depths particularly with glacial retreat along the Antarctic Peninsula revealing areas of rocky substrata for macroalgal colonisation. The confirmed extension of depth where macroalgae can grow will have implications for assessments of benthic productivity and food webs in Antarctica.

Keywords Macrophytobenthos · Molecular phylogeny · Rhodophyta · ROV · Depth limit · Algae · Benthos

Introduction

Antarctic macroalgae have their highest diversity and biomass along the Western Antarctic Peninsula (Wiencke & Amsler 2012), with multiple authors reporting macroalgal communities in the region (Moe & De Laca 1976; Mystikou et al. 2014; Wiencke et al., 2014). Reports relying on direct collection and observation, using SCUBA diving, are limited in depth range to ~30–40 m deep (Mystikou et al. 2014). The

deepest direct macroalgal collection to date has been from 42 m (Delépine et al. 1966). Below these depths macroalgal research has relied on dredge collection and indirect observation such as by Zielinski (1990), who reported the collection of *Desmarestia anceps* and *Himantothallus grandifolius* at depths between 90 and 100 m.

One of the few video observations of algae growing in deeper waters comes from an ROV recording at 70 m depth (Wiencke et al. 2014). Other observations, using dredge and grab samples (Cormaci et al. 2000), found the encrusting red alga *Phymatolithon foecundum* (species complex, Amsler et al. 1995) at 70 m depth. This agrees with previous work on minimum light requirements for Antarctic algae which postulates a physiological limit, which is deeper than 200 m (Wiencke, 1990). Antarctic macroalgae are known to grow at depths of 40 m, but with the potential for deeper growth. This expectation is due to their highly shade-adapted nature (Gómez et al. 2009; Wiencke & Amsler 2012), which allows growth and survival with only half the annual cumulative light exposure of equivalent temperate species (Runcie & Riddle 2006). At these high latitudes sunlight is strongly seasonal, however even during summer (Bischof et al. 2006), when there is 24 h of daylight, sea-ice and the phytoplankton

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bloom can restrict light from reaching the benthos (Clark et al. 2013; Venables & Meredith 2014; Vernet et al. 2008).

Zaneveld (1966, 1968) reported the depth distribution of multiple species, including *Desmarestia menziesii*, from dredge samples from deeper than 650 m, however he argued that such records were undoubtedly algae that had been torn loose by ice scour and drifted into deeper water. As growth at these depths was not supported by physiological data (Gómez et al. 2009; Wiencke & Amsler 2012), and the rate of decay of macroalgal fronds is so low in the cold of the Antarctic (Amsler et al. 1995; Brouwer 1996), the lack of decay does not indicate growth. This lack of decay presents a challenge when trying to establish the depth range of species, as traditional methods and observations cannot definitively determine whether algal specimens are living at deeper depths.

Palmaria decipiens is a common and endemic species in the sublittoral zone of Antarctica (Lamb & Zimmermann 1977; Lüderet al. 2002; Ricker 1988). Typically *P. decipiens* is a “seasonal anticipator” (Lüder et al. 2002), it develops new blades in August following circannual rhythms (Weykam & Wiencke 1996) preparing to grow and reproduce in late winter/spring (Weykam & Wiencke 1996; Wiencke, 1990; Wiencke et al. 1993). Previously collected specimens of *P. decipiens* were dredged from 311 m (J. Zaneveld 1968; J. S. Zaneveld 1966) but, as previously discussed, were considered to contradict theoretical depth limits and it was, therefore, concluded that they had sunk from shallow water (Wiencke, 1990). This study aims to further understand the depth range of *P. decipiens* through photographic surveys and sample collections via ROV, at 100 m depth at Adelaide Island, WAP (Western Antarctic Peninsula).

Materials and methods

Samples were collected from Rothera Point, Adelaide Island, WAP (67° 34' 50" S, 68° 07' 00" W) on steep rocky slopes, adjacent to the Rothera Research Station (British Antarctic Survey), using a Deep Trekker Generation 2 Worker ROV. The ROV allowed individual specimens to be inspected closely and from multiple angles, unlike methods such as video sledges or drop cameras. Each collection dive began with an active search of 1000 m² area for any algae followed by a close-up inspection of any potential specimens. When potential specimens were found, they were manipulated using both the claw and the thrusters of the ROV, with the aim to manipulate the specimen and test whether there are attached. If it required less thrust of the ROV to remove or there was any ambiguity over the outcome, the process was repeated until it could

be confirmed that the specimen was attached, or another specimen was chosen.

Initial morphological examination using the key provided by Wiencke and Clayton (2002) identified the samples as *P. decipiens*. Total genomic DNA was extracted using the Pure-Link™ Genomic DNA Mini Kit (Invitrogen, Waltham, MA, USA), following the manufacturers protocol. PCR fragments were amplified using primer pairs targeting the cytochrome oxidase subunit I (Cox1) gene (Saunders 2005). PCR reactions were performed in 20 µl reaction mixtures containing 10 ng template DNA, using the GoTaq® Green Master Mix (Promega, WI, USA). PCR amplification was applied under the following cycling conditions: an initial denaturation at 95 °C for 10 min followed by 35 cycles. Each cycle included the steps below: a denaturation at 95 °C for 45 s, an annealing at 50 °C for 45 s, and an extension at 72 °C for 1 min. A final extension at 72 °C for 10 min was applied. The PCR amplification Cox1 products were separated in 1.5% (wt/vol) agarose gels using 1X Tris Borate EDTA (TBE) and photographed on a UV transilluminator.

PCR amplification products of both regions were purified using the NucleoSpin Extract Kit (Macherey Nagel, Düren, Germany) in order to remove secondary metabolites prior to sequencing. All sequences were determined on an ABI PRISM® 3700 DNA Analyzer (Applied Biosystems). Each fragment used was sequenced in both directions in order to maximize the accuracy of the sequence.

Results

Several potential specimens were manipulated during the three survey dives (Fig. 1) and they required little force to remove. Two specimens, however, were confirmed as attached macroalgae and could not be easily moved by use of thruster or claw manipulation at 100 m depth. With the claw gripping a section of an algal thallus, it required nearly full thrust to remove a section, indicating that the holdfast attachment to the benthos was secure. These two specimens were collected. Each dive could only collect one specimen and return to the surface at a time. Due to this constraint, multiple specimens that were potentially attached were not collected (Table 1).

Of the two specimens collected from 100 m depth both were identified as *P. decipiens* through taxonomic keys with one being further sampled for sequencing. Phylogenetic data resulted in the aligned cytochrome oxidase subunit I sequence revealed a length of 654 bp (Genbank accession number: No. OL944595). Blast search (Morgulis et al. 2008) revealed that our specimen is 100% identical with *P. decipiens*.

Fig. 1 Video stills from ROV footage during an algal collection at 100 m depth, 31st January 2018 (A, B). High detailed ROV imagery of macroalgae attached on hard substratum at 90 m. February 2016 (C, D). Herbarium specimen (310118-10 FCK) collected via ROV on Jan 2018, scale bar is 5 cm (E)

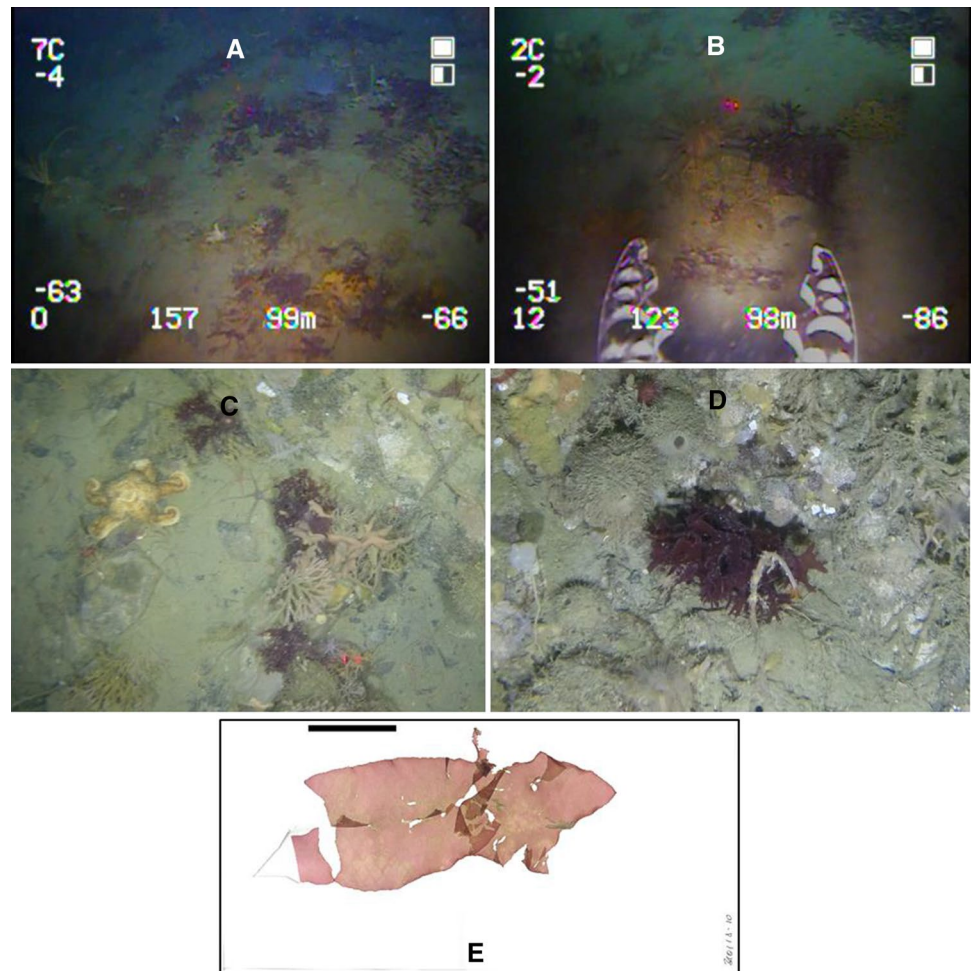


Table 1 Table of rhodophyta specimen collection and testing across 3 ROV dives

Dive #	Depth (m)	Specimens tested	Unattached specimens	Potentially attached	Confirmed attached
1	101	4	2	2	0
2	89	5	1	3	1
3	102	2	1	0	1

Rhodophyta specimens were collect via ROV manipulators, with specimens firmly attached to the seafloor collected (confirmed attached, total: 2). Specimens were collected from Rothera Point, Adelaide Island, WAP (67° 34' 50" S, 68° 07' 00" W)

Discussion

The collection of *P. decipiens* at 100 m depth represents a new depth record for living Antarctic macroalgae. Previous attempts to describe the lower depth limit of *P. decipiens* have been inconclusive and disagreed with their theoretical limit (Gómez et al. 2009; Wiencke & Amsler

2012). *P. decipiens* can propagate at these depths due to being a “seasonal anticipator”, developing new blades in August (Weykam & Wiencke 1996), a time of no or little light at 100 m depth. This life cycle allows it to exploit the short period in late winter/early spring, between the breaking up of the seasonal sea ice and start of light depletion by the phytoplankton bloom, as light requirements for photosynthesis are low and not temperature dependent for this species (Wiencke & Tom Dieck, 1989). ROV dives during this period did observe down welling blue light on low-quality cameras at depths down to 100 m, however the seasonal availability of this down welling light is variable [pers. obs.; (Wiencke, 1990)].

Due to the multiple patches of *P. decipiens* (Fig. 1) being reliably found on each dive (max. 1000 m² area) it is rather unlikely that 100 m depth is the extreme lower limit of this species. Rhodophytes have generally patchy distributions, a characteristic of the Antarctic benthos (Smale 2008; Thrush et al. 2006). Patches of rhodophytes were often found on areas with a gentler slope but this is also a characteristic of fragmented sections of algae collecting in seabed hollows (Braeckman et al. 2019). These

collections exceed previous estimates of 49 ± 22 m depth limit, however it was noted at the time that its depth distribution of macroalgae likely exceeded this (Wiencke 1990). Many specimens that looked attached were often found to be only partially buried fragments (Table 1), which means that previous observations, particularly at depth, may not be able to identify attached and growing algae. *P. decipiens* has variable morphology and although *P. decipiens* was been identified there could be other rhodophytes growing within this depth range.

This source of macroalgal carbon production is an important source of food for the benthic Antarctic community (Huang et al. 2006; Iken et al. 1998). Within Antarctica the shallow (above 40 m depth) hard substrate can be dominated by macroalgae and suspension-feeder assemblages (Quartino et al. 2005; Robinson et al. 2021; Wahl 2009). Through macroalgal decomposition and fragmentation this biomass in the form of macroalgal detritus (or fragments), plays a key role in carbon flux to greater depths or in benthic soft-sediment communities (Cordone et al. 2020; Dunton 2001; Gillies et al. 2012; Norkko et al. 2007, 2004). The establishment of the lower depth limit of algae along the Western Antarctica Peninsula is of particular interest as new suitable rocky substrate is opening up to further macroalgal colonisation (Braeckman et al. 2019), as glacial retreat is occurring at unprecedented rates (A. Cook et al. 2016; A. J. Cook et al. 2015).

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Author contributions BJOR completed the sampling, FCK identified *Palmaria decipiens*, AR, JS, GAG, and AE all contributed to molecular identification and analysis. With BJOR, SMOR, FCK, and GAG contributing to drafting and finalizing the written text.

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Data availability All data can be made available upon request to BJOR (benson@bas.ac.uk).

Declarations

Conflict of interest The authors declare no competing interest.

Ethical approval The authors declare no potential conflict of interests, this research involved no human participants or animals and fully complied with *Polar Biology* ethical standards.

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References

- Amsler CD, Rowley RJ, Laur DR, Quetin LB, Ross RM (1995) Vertical distribution of Antarctic peninsular macroalgae: cover, biomass and species composition. *Phycologia* 34:424–430
- Bischof K, Gomez I, Molis M et al (2006) Ultraviolet radiation shapes seaweed communities. *Rev Environ Sci Biotechnol* 5:141–166
- Braeckman U, Pasotti F, Vázquez S et al (2019) Degradation of macroalgal detritus in shallow coastal Antarctic sediments. *Limnol Oceanogr* 64:1423–1441
- Brouwer PE (1996) Decomposition in situ of the sublittoral Antarctic macroalga *Desmarestia anceps* Montagne. *Polar Biol* 16:129–137
- Clark GF, Stark JS, Johnston EL, Runcie JW, Goldsworthy PM, Raymond B, Riddle MJ (2013) Light-driven tipping points in polar ecosystems. *Glob Change Biol* 19:3749–3761
- Cook AJ, Fox AJ, Vaughan DG, Ferrigno JG (2015) Retreating glacier fronts on the Antarctic Peninsula over the past half-century. *Science* 308:541–544. <https://doi.org/10.1126/science.1104235>
- Cook A, Holland P, Meredith M, Murray T, Luckman A, Vaughan D (2016) Ocean forcing of glacier retreat in the western Antarctic Peninsula. *Science* 353:283–286
- Cordone G, Salinas V, Marina TI, Doyle SR, Pasotti F, Saravia LA, Momo FR (2020) Green vs brown food web: Effects of habitat type on multidimensional stability proxies for a highly-resolved Antarctic food web. *Food Webs* 25:e00166
- Cormaci M, Furnari G, Scammacca B (2000) The macrophytobenthos of Terra Nova Bay. In: Faranda FM, Guglielmo L, Lanora A (eds) Ross sea ecology. Springer, Heidelberg
- Delépine R, Mackenzie LI, Zimmermann MH (1966) Preliminary report on the marine vegetation of the Antarctic Peninsula. *Proc Int Seaweed Sympo* 5:107–116. <https://doi.org/10.1016/B978-0-08-011841-3.50016-1>
- Dunton KH (2001) 15N and 13C measurements of Antarctic Peninsula fauna: trophic relationships and assimilation of benthic seaweeds. *Am Zool* 41:99–112
- Gillies CL, Stark JS, Johnstone GJ, Smith SD (2012) Carbon flow and trophic structure of an Antarctic coastal benthic community as determined by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. *Estuar Coast Shelf Sci* 97:44–57
- Gómez I, Wulff A, Roleda MY et al (2009) Light and temperature demands of marine benthic microalgae and seaweeds in polar regions. *Bot Mar* 52:593–608
- Huang YM, McClintock JB, Amsler CD, Peters KJ, Baker BJ (2006) Feeding rates of common Antarctic gammarid amphipods on ecologically important sympatric macroalgae. *J Exp Mar Biol Ecol* 329:55–65

- Iken K, Quartino M, Barrera-Oro E, Palermo J, Wiencke C, Brey T (1998) Trophic relations between macroalgae and herbivores. *Reports on Polar and Marine Research* 299:258–262
- Lamb IM, Zimmermann MH (1977) Benthic marine algae of the antarctic peninsula: a preliminary guide to the commoner benthic marine algae of the Antarctic Peninsula and Adjacent Islands. American Geophysical Union, Washington, DC
- Lüder UH, Wiencke C, Knoetzel J (2002) Acclimation of photosynthesis and pigments during and after six months of darkness in *Palmaria decipiens* (Rhodophyta): a study to simulate Antarctic winter sea ice cover. *J Phycol* 38:904–913. <https://doi.org/10.1046/j.1529-8817.2002.t01-1-01071.x>
- Moe RL, De Laca TE (1976) Occurrence of macroscopic algae along the Antarctic Peninsula. *Antarct J* 11:20–24
- Morgulis A, Coulouris G, Raytselis Y, Madden TL, Agarwala R, Schäffer AA (2008) Database indexing for production MegaB-LAST searches. *Bioinformatics* 24:1757–1764
- Mystikou A, Peters A, Asensi A et al (2014) Seaweed biodiversity in the south-western Antarctic Peninsula: surveying macroalgal community composition in the Adelaide Island/Marguerite Bay region over a 35-year time span. *Polar Biol* 37:1607–1619. <https://doi.org/10.1007/s00300-014-1547-1>
- Norkko A, Thrush SF, Cummings VJ, Funnell GA, Schwarz AM, Andrew NL, Hawes I (2004) Ecological role of Phyllophora Antarctica drift accumulations in coastal soft-sediment communities of McMurdo Sound, Antarctica. *Polar Biol* 27:482–494
- Norkko A, Thrush S, Cummings V, Gibbs M, Andrew N, Norkko J, Schwarz AM (2007) Trophic structure of coastal Antarctic food webs associated with changes in sea ice and food supply. *Ecology* 88:2810–2820
- Quartino ML, Zaixso HE, Boraso de Zaixso AL (2005) Biological and environmental characterization of marine macroalgal assemblages in potter cove. South Shetland Islands, Antarctica 48:187–197
- Ricker RW (1988) Taxonomy and biogeography of macquarie Island Seaweeds. *British Museum (natural History)* 1:181
- Robinson BJOR, Barnes D GL, Morley S (2021) Intermediate ice scour disturbance is key to maintaining a peak in biodiversity within the shallows of the western Antarctic Peninsula. *Sci Rep* 11:16712
- Runcie JW, Riddle MJ (2006) Photosynthesis of marine macroalgae in ice-covered and ice-free environments in east Antarctica. *Eur J Phycol* 41:223–233
- Saunders GW (2005) Applying DNA barcoding to red macroalgae: a preliminary appraisal holds promise for future applications. *Philos Trans R Soc Lond B Biol Sci* 360:1879–1888
- Smale D (2008) Spatial variability in the distribution of dominant shallow-water benthos at Adelaide Island, Antarctica. *J Exp Mar Biol and Ecol* 357:140–148. <https://doi.org/10.1016/j.jembe.2008.01.014>
- Thrush S, Dayton P, Cattaneo-Vietti R et al (2006) Broad-scale factors influencing the biodiversity of coastal benthic communities of the Ross Sea. *Deep-Sea Res II: Top Stud Oceanogr* 53:959–971. <https://doi.org/10.1016/j.dsr2.2006.02.006>
- Venables HJ, Meredith MP (2014) Feedbacks between ice cover, ocean stratification, and heat content in Ryder Bay, western Antarctic Peninsula. *J Geophys Res* 119:5323–5336. <https://doi.org/10.1002/2013jc009669>
- Vernet M, Martinson D, Iannuzzi R et al (2008) Primary production within the sea-ice zone west of the Antarctic Peninsula: i—Sea ice, summer mixed layer, and irradiance. *Deep-Sea Res II: Top Stud Oceanogr* 55:2068–2085. <https://doi.org/10.1016/j.dsr2.2008.05.021>
- Wahl M (2009) Habitat characteristics and typical functional groups. In: Wahl M (ed) *Marine hard bottom communities*. Springer, Heidelberg, pp 7–17
- Wiencke C, Dieck TI (1989) Temperature requirements for growth and temperature tolerance of macroalgae endemic to the Antarctic region. *Mar Ecol Prog Ser* 47:167. <https://doi.org/10.1007/bf024303>
- Wiencke C (1990) Seasonality of red and green macroalgae from Antarctica—a long-term culture study under fluctuating Antarctic daylengths. *Polar Biol* 10:601–607
- Weykam G, Wiencke C (1996) Seasonal photosynthetic performance of the endemic antarctic red alga *Palmaria decipiens* (Reinsch) ricker. *Polar Biol* 16:357–361. <https://doi.org/10.1007/bf02342184>
- Wiencke C, Rahmel J, Karsten U, Weykam G, Kirst G (1993) Photosynthesis of marine macroalgae from Antarctica: light and temperature requirements. *Botanica Acta* 106:78–87
- Wiencke C, Clayton MN (2002) *Antarctic Seaweeds*. A. R. G. Gantner, Ruggell
- Wiencke C, Amsler CD (2012) Seaweeds and their communities in polar regions. In: Wiencke C (ed) *Bischof, Seaweed Biology*. Springer, Bremerhaven, pp 265–291
- Wiencke C, Amsler C, Clayton M (2014) Macroalgae. In: De Broyer C, Koubbi P, Griffiths HJ (eds) *Biogeographic atlas of the Southern Ocean*. Scientific Committee on Antarctic Research, Cambridge, pp 66–73
- Zaneveld JS (1966) The occurrence of benthic marine algae under shore fast-ice in the western Ross Sea, Antarctica. Paper presented at the Proceedings of the Fifth International Seaweed Symposium, Halifax, August 25–28, 1965.
- Zaneveld J (1968) Benthic marine algae, Ross Island to Balleny Islands. *Primary Productivity and Benthic Marine Algae of the Antarctic and Subantarctic Antarctic Map Folio Series, Folio* 10:10–12
- Zielinski K (1990) Bottom macroalgae of the Admiralty Bay (King George Island, South Shetlands, Antarctica). *Pol Polar Res* 11:95–131

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