

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

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39 **Abstract**

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

51 **Keywords:** Macrophytobenthos, molecular phylogeny, Rhodophyta, ROV, Depth limit, Algae, Benthos

52 **Introduction**

53 Antarctic macroalgae have their highest diversity and biomass along the Western Antarctic Peninsula (Christian
54 Wiencke & Amsler, 2012), with multiple authors reporting macroalgal communities in the region (Moe & De
55 Laca, 1976; Mystikou et al., 2014; Christian Wiencke, Amsler, & Clayton, 2014). Reports relying on direct
56 collection and observation, using SCUBA diving, are limited in depth range to ~30-40 m deep (Mystikou et al.,
57 2014). The deepest direct macroalgal collection to date has been from 42 m (Delépine, Mackenzie, &
58 Zimmermann, 1966). Below these depths macroalgal research has relied on dredge collection and indirect
59 observation such as by Zielinski (1990), who reported the collection of *Desmarestia anceps* and *Himantothallus*
60 *grandifolius* at depths between 90-100 m.

61 One of the few video observations of algae growing in deeper waters comes from an ROV recording at 70 m
62 depth (Christian Wiencke et al., 2014). Other observations, using dredge and grab samples (Cormaci, Furnari, &
63 Scammacca, 2000), found the encrusting red alga *Phymatolithon foecundum* (species complex, Amsler, Rowley,
64 Laur, Quetin, & Ross, 1995) at 70 m depth. This agrees with previous work on minimum light requirements for
65 Antarctic algae which postulates a physiological limit, which is deeper than 200 m (Christian Wiencke, 1990a,
66 1990b). Antarctic macroalgae are known to grow at depths of 40 m, but with the potential for deeper growth.
67 This expectation is due to their highly shade-adapted nature (Gómez et al., 2009; Christian Wiencke & Amsler,
68 2012), which allows growth and survival with only half the annual cumulative light exposure of equivalent
69 temperate species (Runcie & Riddle, 2006). At these high latitudes sunlight is strongly seasonal, however even
70 during summer (Bischof et al., 2006), when there is 24 hours of daylight, sea-ice and the phytoplankton bloom
71 itself can restrict light from reaching the benthos (Clark et al., 2013; Venables & Meredith, 2014; Vernet et al.,
72 2008).

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

81 *Palmaria decipiens* is a common and endemic species in the sublittoral zone of Antarctica (Lamb &
82 Zimmermann, 1977; Lüderet al., 2002; Ricker, 1987). Typically *P. decipiens* is a “seasonal anticipator” (Lüder
83 et al., 2002), it develops new blades in August following circannual rhythms (Weykam & Wiencke, 1996)
84 preparing to grow and reproduce in late winter/spring (Weykam & Wiencke, 1996; Christian Wiencke, 1990b;
85 Christian Wiencke, Rahmel, Karsten, Weykam, & Kirst, 1993). Previously collected specimens of *P. decipiens*
86 were dredged from 311 m (J. Zaneveld, 1968; J. S. Zaneveld, 1966) but, as previously discussed, were
87 considered to contradict theoretical depth limits and it was, therefore, concluded that they had sunk from
88 shallow water (Christian Wiencke, 1990b). This study aims to further understand the depth range of *P. decipiens*

89 through photographic surveys and sample collections via ROV, at 100 m depth at Adelaide Island, WAP
90 (Western Antarctic Peninsula).

91 **Materials and Methods**

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

101 Initial morphological examination using the key provided by Wiencke and Clayton (2002) identified the
102 samples as *P. decipiens*. Total genomic DNA was extracted using the PureLink™ Genomic DNA Mini Kit
103 (Invitrogen, Waltham, MA, USA), following the manufacturers protocol. PCR fragments were amplified using a
104 primer pairs targeting the cytochrome oxidase subunit I (Cox1) gene (Saunders, 2005). PCR reactions were
105 performed in 20 µl reaction mixtures containing 10 ng template DNA, using the GoTaq® Green Master Mix
106 (Promega, WI, USA). PCR amplification was applied under the following cycling conditions: an initial
107 denaturation at 95°C for 10 min followed by 35 cycles. Each cycle included the steps below: a denaturation at
108 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
109 10 min was applied. The PCR amplification products were separated in 1.5% (wt/vol) agarose gels using 1X
110 Tris Borate EDTA (TBE) and photographed on a UV transilluminator.

111 PCR amplification products of both regions were purified using the NucleoSpin Extract Kit (Macherey Nagel,
112 Düren, Germany) in order to remove secondary metabolites prior to sequencing. All sequences were determined
113 on an ABI PRISM® 3700 DNA Analyzer (Applied Biosystems). Each fragment used was sequenced in both
114 directions in order to maximize the accuracy of the sequence. Additional sequences from other species within
115 the *Palmariales* order were derived from the NCBI database (GenBank®—www.ncbi.nlm.nih.gov/ (accessed on
116 15 December 2021) (Tab. 1). In an attempt to polarize the reconstruction of the phylogenetic tree in the present
117 study we inferred *Plocamium maggsiae* (*Plocamiales*) as outgroup. All data sets were aligned and converted for
118 further analysis using the AliView software (Larson & Grace, 2004). Phylogenetic relationships were inferred
119 MrBayes v.2.01 software was used for Bayesian inference (Huelsenbeck & Ronquist, 2001). The three
120 respective tree spaces were explored using four chains: one cold chain and subsequently three incrementally
121 heated ones by temperature set at 0.20. A GTR model of sequence evolution was employed allowing a gamma
122 shape of among-site rate variation. Posterior probability distributions were obtained for the phylogenies and the
123 parameters of the model of sequences' evolution were adjusted; random trees were used as seeds. Tree spaces
124 were explored inferring 1,000,000 generations with the burn-in at 25% of generations.

125 **Results**

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

132 Phylogenetic data resulted in the aligned cytochrome oxidase subunit I sequence revealed a length of 654 bp
133 (Genbank accession number: No. OL944595). Blast search (Morgulis et al., 2008) revealed that our specimen is
134 100% identical with *P. decipiens*. Among the available deposit sequences for Cox1 region, the phylogenetic tree
135 (Fig. 2) was calculated and the supported clades showed paraphyly within the genus *Palmaria*.

136 **Discussion**

137 The collection of *P. decipiens* at 100 m depth represents a new depth record for living Antarctic macroalgae.
138 Previous attempts to describe the lower depth limit of *P. decipiens* have been inconclusive and disagreed with

139 their theoretical limit (Gómez et al., 2009; Christian Wiencke & Amsler, 2012). *P. decipiens* can propagate at
140 these depths due to being a “seasonal anticipator”, developing new blades in August (Weykam & Wiencke,
141 1996), a time of no or little light at 100 m depth. This life cycle allows it to exploit the short period in late
142 winter/early spring, between the breaking up of the seasonal sea ice and start of light depletion by the
143 phytoplankton bloom, as light requirements for photosynthesis are low and not temperature dependent for this
144 species (Christian Wiencke & Tom Dieck, 1989). ROV dives during this period did observe downwelling blue
145 light on low-quality cameras at depths down to 100 m, however the seasonal availability of this down-welling
146 light is variable (pers. obs.; (Christian Wiencke, 1990a, 1990b)).

147 Due to the multiple patches of *P. decipiens* (Fig. 1) being reliably found on each dive (max. 1000 m² area) it is
148 rather unlikely that 100 m depth is the extreme lower limit of this species. Rhodophytes have generally patchy
149 distributions, a characteristic of the Antarctic benthos (Smale, 2008; Thrush et al., 2006). Patches of
150 rhodophytes were often found on areas with a gentler slope but this is also a characteristic of fragmented
151 sections of algae collecting in seabed hollows (Braeckman et al., 2019). These collections concur with the
152 previously estimated ~150 m depth limit (Christian Wiencke, 1990a, 1990b). Many specimens that looked
153 attached were often found to be only partially buried fragments (Tab. 2), which means that previous
154 observations, particularly at depth, may not be seeing attached and growing algae. Not all macroalgae observed
155 were likely *P. decipiens* as they showed varying morphology and although *P. decipiens* was been identified is
156 unlikely the only rhodophyte with this depth range.

157 This source of macroalgal carbon production is an important source of food for the benthic Antarctic community
158 (Huang, McClintock, Amsler, Peters, & Baker, 2006; Iken et al., 1998). Within Antarctica the shallow (above
159 40 m depth) hard substrate can be dominated by macroalgae and suspension-feeder assemblages (Quartino,
160 Zaixso, & Boraso de Zaixso, 2005; Robinson, Barnes, Grange, & Morley, 2021; Wahl, 2009). Through
161 macroalgal decomposition and fragmentation, this biomass in the form of macroalgal detritus (or fragments),
162 plays a key role in carbon flux to greater depths or in benthic soft-sediment communities (Cordone et al., 2020;
163 Dunton, 2001; Gillies et al., 2012; Norkko et al., 2007; Norkko et al., 2004). The establishment of the lower
164 depth limit of algae along the Western Antarctica Peninsula is of particular interest as new suitable rocky
165 substrate is opening up to further macroalgal colonisation (Braeckman et al., 2019), as glacial retreat is
166 occurring at unprecedented rates (A. Cook et al., 2016; A. J. Cook, Fox, Vaughan, & Ferrigno, 2015).

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171 **Competing Interests**

172 The authors declare no competing interests

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179 **Author Contributions**

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

183 **Compliance with Ethical Standards**

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

186 **Data availability**

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

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