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SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

► CHAPTER 5.1. MACROALGAE.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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5.1. Macroalgae

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1. Introduction

Research on Antarctic macroalgae began with the expeditions of Gaudichaud, Bory, Montagne, Hooker and Harvey as early as 1817 (Godley 1965). A second notable period in the exploration of macroalgae from the Southern Ocean and the cold-temperate regions of South America was around the turn of the 19th to the 20th century. The most important studies during this time were conducted by Hariot, Reinsch, Gain, Skottsberg and Kylin (Wiencke & Clayton 2002). These taxonomic and biogeographical studies enabled Papenfuss (1964) to produce the first catalogue of Antarctic and sub-Antarctic benthic marine macroalgae. The introduction of SCUBA diving into the methodological portfolio by Neushul (1965), Zaneveld (1966a, b, 1968) and Delépine *et al.* (1966) opened a new era. Later on, Moe (Moe & DeLaca 1976), Lamb & Zimmermann (1976), Amsler (Amsler *et al.*, 1995) and Klöser and co-workers (Klöser *et al.* 1996) conducted numerous diving studies allowing for the first time more precise descriptions of the depth distribution of Antarctic macroalgae. In subsequent years a major attempt was made to investigate the life history of Antarctic species (Wiencke *et al.* 2007). In this period scientific knowledge of Antarctic macroalgae was considerably broadened and the first monograph of these ecologically important species was compiled (Wiencke & Clayton 2002). Moreover, in-depth studies on the physiological thallus anatomy (Wiencke *et al.* 2007), phenology (Wiencke *et al.* 2011) as well as on the temperature and light requirements (Gómez *et al.* 2011, Wiencke & Amsler 2012) of Antarctic species became possible. Detailed investigations on trophic relations between macroalgae and herbivores began in the last decade of the 20th century (Iken 1996, 1999). Recent studies focus on the defenses between macroalgae and herbivores, defences against diatom fouling (Amsler *et al.* 2005a, 2008, 2011, Iken *et al.* 2011, Wiencke & Amsler 2012) as well as on the effect of global climate changes on geographic distribution (Müller *et al.* 2011) and depth zonation (Zacher *et al.* 2007a, Campana *et al.* 2011).



Photo 1 *Desmarestia antarctica* R.L. Moe & P.C. Silva and *Himantothallus grandifolius* (A. Gepp & E.S. Gepp) Zinova. Ardley Peninsula, Fildes Bay (King George Island). Image: J. Holtheuer © Universidad Austral de Chile in Valdivia.

2. Biodiversity of Antarctic macroalgae

Our knowledge of the biodiversity of Antarctic macroalgae is still hampered by the limited database available. In particular, a great part of the East Antarctic coast between 45°E and 160°E is certainly under-sampled. Many records are only based on dredged or drift specimens, which are of limited usefulness or are doubtful because they have been sampled only very few times and may have been confused with morphologically similar species. Therefore, a precise estimation of the number of species of Antarctic macroalgae is difficult. Skottsberg (1964) listed 96 species, whereas Wiencke & Clayton (2002) recognised at least 119 species. Only recently, five more species were described (Hommersand *et al.* 2011). Compared to the temperate and tropical regions of the world this is, however, a low species richness, but in a similar range as in the Arctic (Wulff *et al.* 2011). The degree of endemism is high in the Antarctic marine flora (Clayton 1994) with highest levels in the Heterokontophyta and the Rhodophyta (Table 1). Within the Phaeophyceae there is one endemic order, the Ascoseirales, comprising one species only, the kelp-like *Ascoseira mirabilis* Skottsberg (Map 8). The order Desmarestiales has its evolutionary origin in the Southern Hemisphere (Peters *et al.* 1997) and in Antarctica species of this order occupy the same ecological niche as the order Laminariales (which is absent from Antarctica) in the Northern Hemisphere. There are numerous endemic genera, among the Phaeophyceae: *Himantothallus* Skottsberg (Map 1), *Phaeurus* Skottsberg and *Cystosphaera* Skottsberg (Map 9), among the Rhodophyta: *Notophycus* R.L.Moe, *Microrhinus* Skottsberg, *Hymenocladopsis* R.L.Moe, *Nereoginkgo* Kylin, *Antarcticothamnion* R.L.Moe & P.C.Silva, *Gainia* R.L.Moe, *Rhodokrambe* R.L.Moe, *Leniea* R.L.Moe, *Austropugetia* R.L.Moe and

Varimenia R.L.Moe, and among the Chlorophyta: *Lambia* Delépine (Map 10) and *Lola* A.Hamel & G.Hamel. Species of most of these genera occur in the Antarctic Peninsula region (West Antarctica) only, *Himantothallus grandifolius* (A. & E. Gepp) Zinova and *Georgiella confluens* (Reinsch) Kylin (Map 3) occur both in West and East Antarctica, *Lola irregularis* Zaneveld occurs in East Antarctica only. So West Antarctica is — in contrast to East Antarctica — clearly a macroalgal hotspot. Whether this pattern is the result of incomplete collecting, incomplete dispersal or not remains to be studied.

Table 1 Levels of endemism in Antarctic macroalgae (after Wiencke & Clayton 2002; including Hommersand *et al.* 2011).

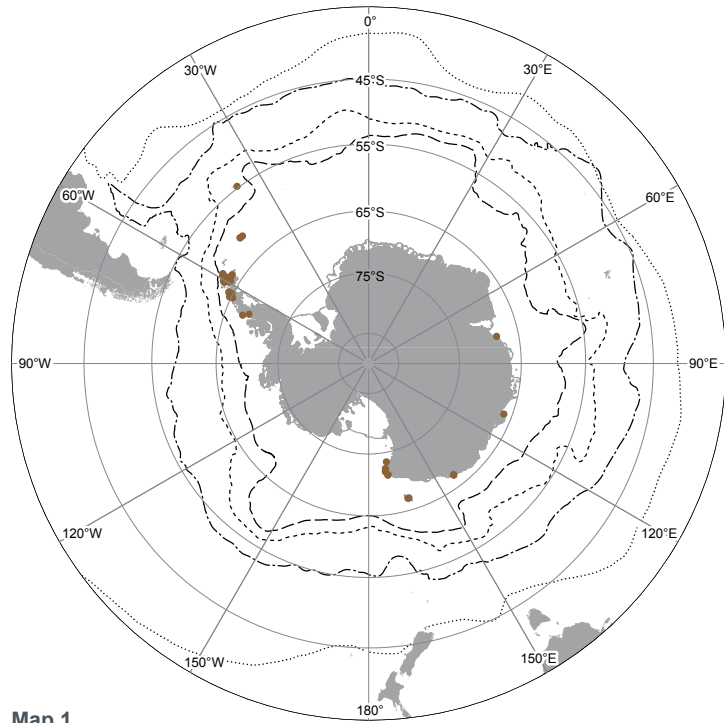
	N. species	N. endemic species	% endemic
Rhodophyta	80	29	36
Heterokontophyta	27	12	44
Chlorophyta	17	3	18
Total	124	44	35

3. Composition and depth distribution of seaweed communities

The most diverse macroalgal communities with the highest biomass occur in the shallow subtidal zone along the northern and central areas of the western Antarctic Peninsula (Wiencke & Amsler 2012). Numerous authors have reported on the cover and/or biomass of macroalgal communities in this region (Neushul 1965, Delépine *et al.* 1966, DeLaca & Lipps 1976, Richardson 1979, Zieliński 1981, 1990, Chung *et al.* 1994, Klöser *et al.* 1994, 1996, Amsler *et al.* 1995, Brouwer *et al.* 1995, Quartino *et al.* 2001, 2005, Quartino & Boraso de Zaixso 2008) and the following description of the zonation of brown, red, and green macroalgae on the western Antarctic Peninsula is a summary of these reports combined with our personal observations of the flora over many years. Throughout the region, large, perennial brown macroalgae usually dominate in terms of both biomass and percent cover of the bottom, with *Desmarestia menziesii* J.Agardh (Map 2), *Desmarestia anceps* Montagne (Map 7) and *Himantothallus grandifolius* (Map 1) usually reported as most common. Specific zonation patterns of the dominant brown algae vary with site, but the overall pattern is relatively consistent among these reports from multiple sites and years. The upper 2–3 m of the subtidal is typically heavily impacted by ice scour and, with the exception of well protected spots, rarely supports these large perennial algae. Below this heavy scour area, *D. menziesii* commonly becomes abundant and then grades into and is eventually replaced at greater depths by *D. anceps*. At some locations, however, only one of these two *Desmarestia* species is present, at least in quantity. Unfortunately, because they are very similar morphologically, some reports have lumped these species together, thereby obscuring any patterns. Below the zone dominated by *Desmarestia* spp., the large, blade-forming *H. grandifolius* becomes dominant. The depths at which these transitions between dominant species occur vary widely between sites, as will be discussed further below.

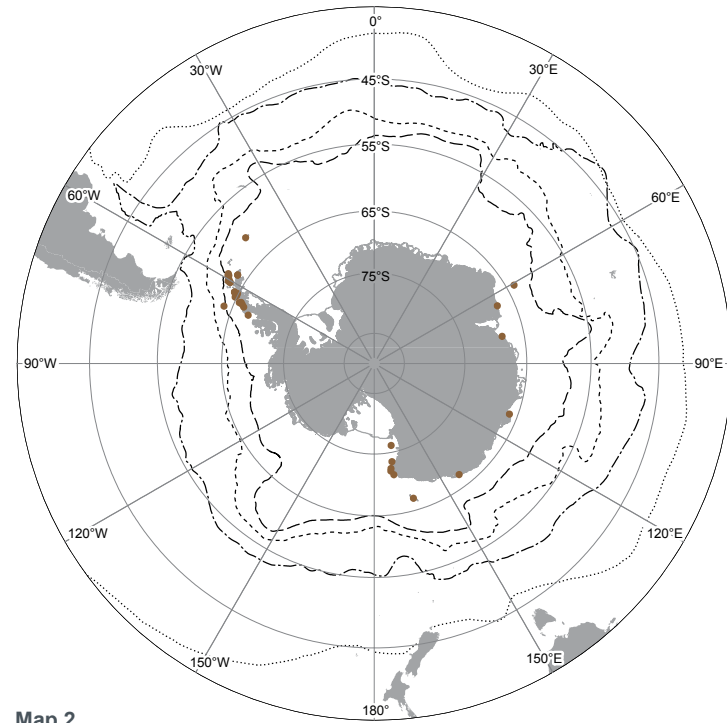
Several other large brown macroalgae can occasionally co-dominate with these three most common species. *Ascoseira mirabilis* (Map 8) is sometimes reported to replace or co-dominate with *D. menziesii* at shallow depths although it can also occur deeper (Chung *et al.* 1994, Klöser *et al.* 1996, Quartino *et al.* 2001). *Desmarestia antarctica* R.L.Moe & P.C.Silva is a relatively fast growing annual or biennial species that can occasionally be locally dominant in the zone typical of *D. anceps* (Chung *et al.* 1994, Amsler *et al.* 1995, Quartino *et al.* 2001). Quartino *et al.* (2001) have suggested that this represents a temporary situation in areas where the competitively dominant *D. anceps* has recently been removed by ice scour. This is consistent with our personal observations (Amsler) of areas that have returned to *D. anceps* dominance after previously having been dominated by *D. antarctica* (e.g., Amsler *et al.* 1995). At greater depths where ice scour is less common, *Cystosphaera jacquinotii* (Map 9) can become co-dominant with or locally replace *D. anceps* and/or *H. grandifolius* (Amsler personal observations, Zieliński 1981, Klöser *et al.* 1996). The small brown alga, *Adenocystis utricularis* (Bory) Skottsberg (Map 13) is a pioneer species and can be common in frequently ice scoured areas of the very shallow subtidal and in intertidal cracks and crevices (e.g., Neushul 1965, DeLaca & Lipps 1976, Zieliński 1981, Chung *et al.* 1994).

Although this overall zonation pattern of large brown algae is consistent across the above referenced reports, the maximum reported depths of the macroalgal community and the specific depth zonation ranges of the dominant brown macroalgae vary widely. Clearly, the overall depth range is constrained by available light, with the range extending deeper in relatively exposed areas with clearer, open ocean water compared to relatively protected areas with greater turbidity due to glacial melt and/or with more frequent ice cover (Amsler personal observations, DeLaca & Lipps 1976, Brouwer *et al.* 1995). Zieliński (1990) reported maximum depths of 90–100 m for *D. anceps* and *H. grandifolius*. However, these reports were based on dredged material, not direct observations. It is likely that at least some of the algae collected this way at great depth represent individuals dislodged from shallower water by ice scour, rafted on their rock substrates to greater depths via ice, and



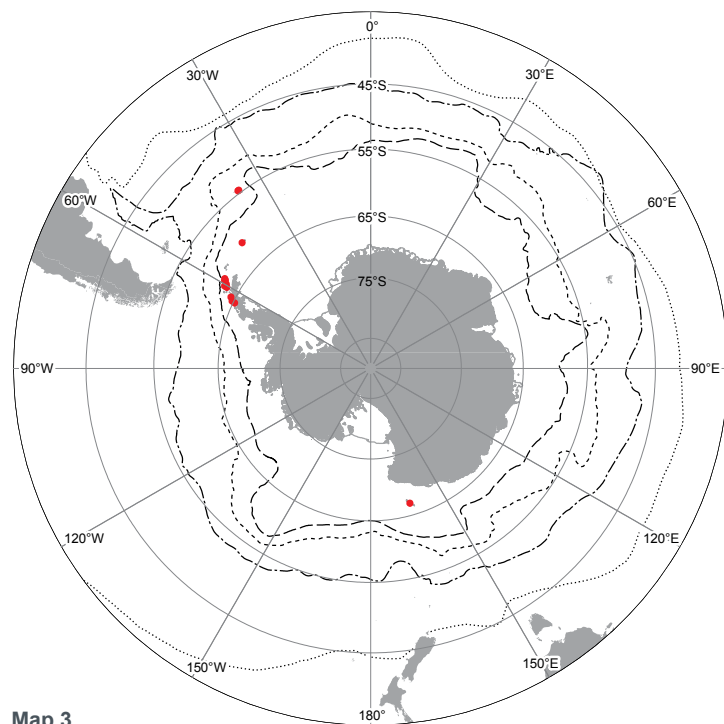
Map 1

● *Himantothallus grandifolius*



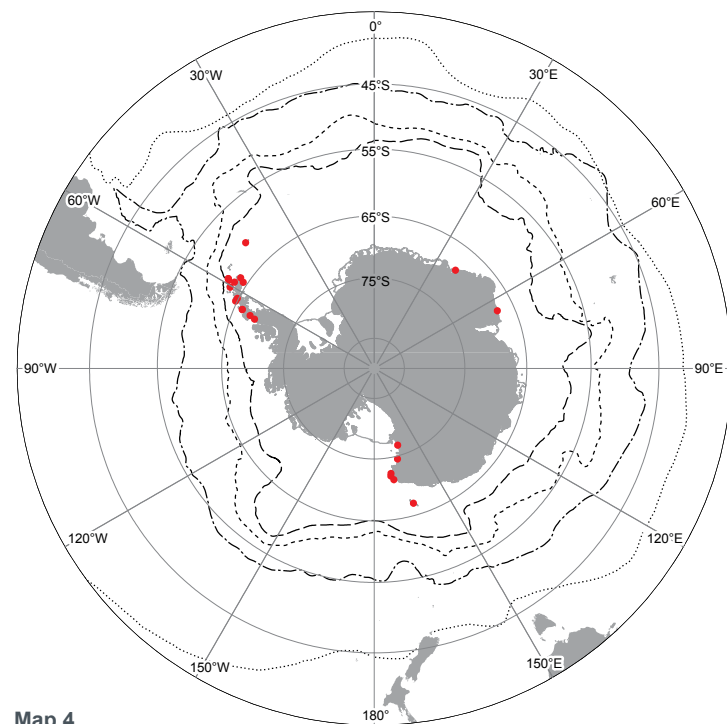
Map 2

● *Desmarestia menziesii*



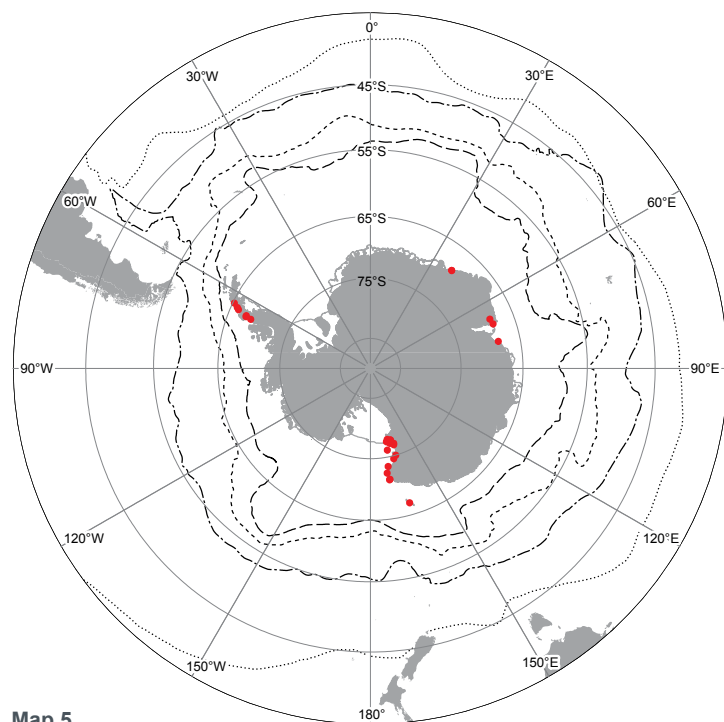
Map 3

● *Georgiella confluens*



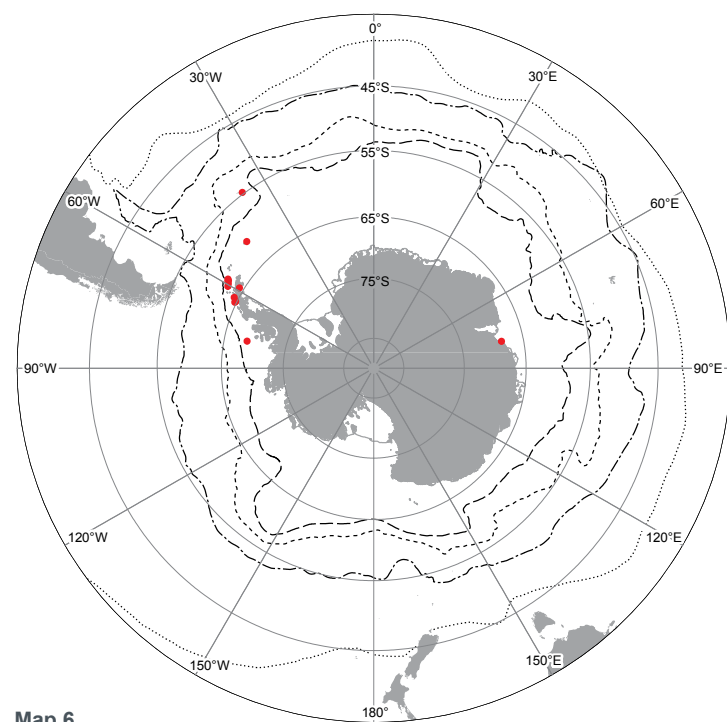
Map 4

● *Phycodrys antarctica*



Map 5

● *Phyllophora antarctica*



Map 6

● *Porphyra endiviifolia*

Macroalgae Maps 1–6 Endemic Antarctic species with a circum-Antarctic distribution: Map 1. The brown alga *Himantothallus grandifolius*. Map 2. The brown alga *Desmarestia menziesii*. Map 3. The red alga *Georgiella confluens*. Map 4. The red alga *Phycodrys antarctica*. Map 5. The red alga *Phyllophora antarctica*. Map 6. The red alga *Porphyra endiviifolia*.

which remained apparently fresh and healthy in the cold, oxygen-rich Antarctic waters. Attached *H. grandifolius* has, however, been observed down to 70 m depth on South Georgia on video recordings made by use of a remotely operated vehicle (Wiencke & Bergström unpublished). These observations fit well to estimates based on physiological studies on the minimum light requirements of Antarctic macroalgae (Wiencke 1990a, 1990b).

Several authors have considered why the depth zonation patterns of dominant brown algae vary so much, particularly with respect to the transition between *D. anceps* and *H. grandifolius* (Richardson 1979, Klöser *et al.* 1994, 1996, Brouwer *et al.* 1995, Quartino *et al.* 2001). Differential resistance to grazing has been hypothesised to perhaps have a role, but more recent studies have demonstrated that all of these large brown macroalgae are unpalatable to a variety of potential consumers because of the production of chemical defenses (Amsler *et al.* 2005, 2011, Wiencke & Amsler 2012, R.E. McDowell & Amsler unpublished). *D. anceps* and *D. menziesii* appear to be competitively dominant to *H. grandifolius* under ideal conditions (Klöser *et al.* 1994) and wave exposure, substrate type, and bottom topography all seem to influence when one versus another species will dominate in a particular location (summarised by Klöser *et al.* 1996). For example, on bedrock or bolder substrates with moderate or calm wave exposure, *H. grandifolius* commonly predominates in areas with vertical topography while *D. anceps* commonly predominates in areas with sloping or horizontal topography (Klöser *et al.* 1996). However, as discussed by Klöser *et al.* (1994, 1996), these factors probably do not completely explain the distributions, particularly with respect to the depth at which dominance transitions from *D. anceps* to *H. grandifolius*. Indeed, based on personal observations (Amsler) during nearly 650 scuba dives near Palmer Station on Anvers Island (64°46'S, 64°03'W), although many sites match the general patterns described by Klöser *et al.* (1996), others do not. For example, in areas with moderate wave exposure and bedrock substrates, one can find gently sloping sites which are dominated by *H. grandifolius* from less than 10 m to over 30 m depth as well as other sites with vertical topography which are dominated by *D. anceps* over this same depth range. It seems likely that other, yet to be discerned factors also influence these distributions over local scales.

Red macroalgae are reported as common in the western Antarctic Peninsula subtidal in all the studies listed above although they only rarely dominate in terms of biomass or cover at any depth. The most common exception to this is *Palmaria decipiens* (Reinsch) R.W.Ricker (Map 17), which can be a dominant or co-dominant species in shallow waters, particularly in relatively protected areas with gently sloping topography (Amsler personal observations, DeLaca & Lipps 1976, Chung *et al.* 1994, Klöser *et al.* 1996). The species also grows as a pioneer species in newly ice-free areas with high sediment loads until at least 10 m depth (Deregibus pers. communication). Other fleshy red macroalgae that are commonly reported in the above-listed publications as important components of the subtidal flora at various sites and depths are *Iridaea cordata* (Turner) Bory (Map 18), *Gigartina skottsbergii* Setchell & N.L.Gardner (Map 14), *Myriogramme manginii* (Gain) Skottsberg (Map 11), *Plocamium cartilagineum* (Linnaeus) P.S.Dixon (Map 15) and, occasionally, *Georgiella confluens* (Map 4). Both calcified and uncalcified encrusting red macroalgae are common and can cover >70% of the rock substrate across a wide depth range beneath the larger, fleshy brown and red macroalgae (Amsler *et al.* 1995).

Free-living green macroalgae are relatively uncommon in reports from the western Antarctic Peninsula subtidal. *Lambia antarctica* (Map 10) is rarely reported but can occur in deeper waters, particularly where there is a light covering of sediment on the rocky substrate (Amsler personal observations, DeLaca & Lipps 1976). The green macroalga most commonly reported in the subtidal is *Monostroma harti* Gain (Map 16) which can also be common in the intertidal. Klöser *et al.* (1996) concluded that subtidal *M. harti* represents a pioneer species in areas of recent, heavy ice scour although it has occasionally also been reported as an epiphyte on larger brown macroalgae (e.g. Neushul 1965). By comparison it is of note that one of us (Amsler) does not recall ever having observed it in the subtidal over many hundreds of scuba dives at Anvers Island even though it does occur there in the intertidal.

Many of the foregoing reports from the western Antarctic Peninsula include descriptions of the intertidal, at least in terms of species presence (see also Hedgpeth 1969, Lamb & Zimmermann 1977, Gallardo *et al.* 1999, Kim 2001). Green macroalgae including *M. harti*, *Ulva hookeriana* (Kützinger) Hayden, Blomster, Maggs, P.C., M.J.Stanhope & J.R.Waaland (Map 18), *Urospora penicilliformis* (Roth) Areschoug (Map 15) and *Ulothrix* spp. are commonly reported. Likewise, the supralittoral red alga *Porphyra endiviifolia* (A. & E.S. Gepp) Chamberlain (Map 6) has been frequently collected. In addition to these, shallow subtidal species including the red algae *I. cordata* and *Curdiea racovitzae* Hariot and the brown alga *A. utricularis* are often reported to occur in tide pools.

Although filamentous green macroalgae such as *U. penicilliformis* and species of the genus *Ulothrix* Kützinger are common in the western Antarctic Peninsula intertidal, a unique feature of the subtidal is the almost complete absence of free living, filamentous algae throughout most of the year coupled with the very common occurrence of filamentous green and brown algae growing as endophytes in the larger brown and red macroalgae (Peters 2003, Amsler *et al.* 2009). Peters (2003) hypothesised that this is the result of the dense mesograzers fauna, particularly amphipods, in these communities (cf. Richardson 1971, 1975, Huang *et al.* 2007). Recent studies have supported this hypothesis. Amsler *et al.* (2009) reported that the endophytes themselves are very palatable to amphipods and will grow out from their hosts in amphipod-free culture. Aumack *et al.* (2011) showed that endophytes also grow out and become epiphytic on their hosts when held without amphipods in experimental

mesocosms. Amsler *et al.* (2012a) demonstrated that intertidal green algae are rapidly consumed by amphipods when transplanted to subtidal macroalgal communities.

There are far fewer reports on the distribution of Antarctic macroalgae from regions outside the Antarctic Peninsula. The most detailed reports are from the Ross Sea, particularly from Terra Nova Bay (Gambi *et al.* 1994, Cattaneo-Vietti *et al.* 2000, Cormaci *et al.* 2000) and McMurdo Sound (Miller & Pearse 1991). These areas are dominated by the fleshy red algae *I. cordata* (Map 18) and *Phyllophora antarctica* A. & E.S. Gepp (Map 5) and by the crustose coralline alga *Phymatolithon foecundum* L. Düwel & S. Wegeberg. *I. cordata* dominates between 2 and 10 m with *P. antarctica* most common from 10 to 20 m. *P. foecundum* as currently understood includes coralline algae previously reported as several different species (Alongi *et al.* 2002) and occurs to depths of 70 m (Cormaci *et al.* 2000). Although these are the only three species reported as present throughout the year in the more southerly limits of worldwide macroalgal distribution at McMurdo Sound (Miller & Pearse 1991), other species including the red algae *Phycodrys antarctica* (Map 4) and *P. cartilagineum* (Map 15) and the green algae *M. harti* (Map 18) and *U. penicilliformis* (Map 15) also occur in Terra Nova Bay (Cormaci *et al.* 1992). Zaneveld (1966a, b) reported on these same areas as well as more northerly areas of the Ross Sea where additional species such as *H. grandifolius* (Map 1) *D. menziesii* (Map 2), and *P. decipiens* (Map 17) also occur. Zaneveld (1966a, b) reports depth distributions based on dredge samples of several species in excess of 150 m including *D. menziesii* at depths exceeding 650 m. Although Zaneveld argued against it, such records undoubtedly represent algae which were torn loose and rafted from shallower waters by ice. Although Antarctic macroalgae are extremely shade adapted (Gómez *et al.* 2011, Wiencke & Amsler 2012) growth of macroalgae at these extraordinary depths are not supported by physiological data. Although the algal samples from Zaneveld appeared fresh, it has to taken into account that the decomposition rate of macroalgal fronds is very low in Antarctic waters, as exemplified for *D. anceps* at Signy Island. Fronds of this species fixed in nylon net bags at 12 m depth on the seafloor remained healthy and did not lose weight during 144 days of exposure. Only after 313 days a weight loss of 40% became apparent (Brouwer 1996). Amsler *et al.* (2012b) reported similar results for detached *D. anceps* from Anvers Island held for over 300 days in a zone of macroalgal drift material at 17 m depth.

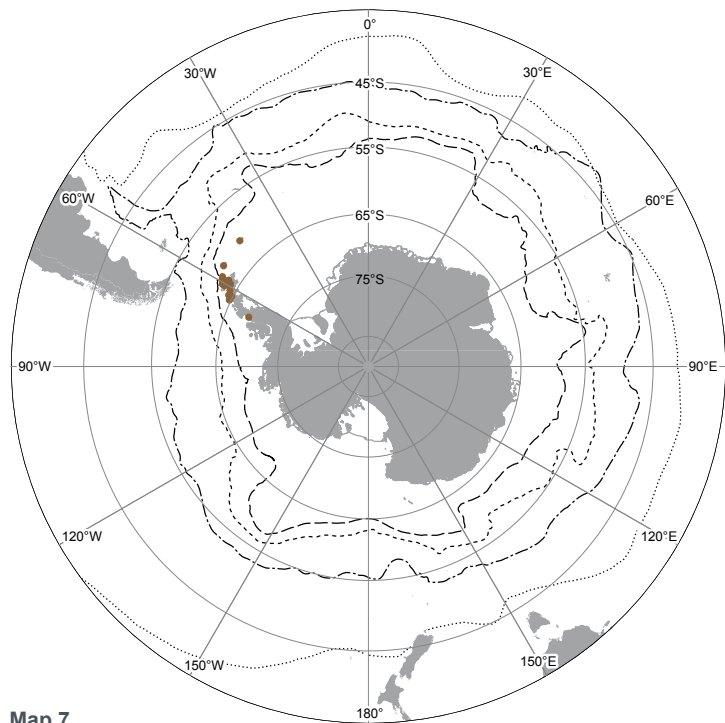
Macroalgal depth distribution reports are available from only two areas in East Antarctica, the Windmill Islands (66°18'S, 110°27'E) and the Vestfold Hills (68°30'S, 70°00'E). In areas of the Windmill Islands where sea ice breaks out in the spring, *P. decipiens* and *D. menziesii* dominate at 6 m while *H. grandifolius* is dominant at 12 m depth with *P. cartilagineum* as the most common fleshy understory species at both depths (Johnston *et al.* 2007, Clark *et al.* 2011). Crustose coralline red algae can cover over 70% of the substrate under fleshy macroalgal canopies at this location (Irving *et al.* 2005). The Vestfold Hills report of Kirkwood & Burton (1988) focuses primarily on benthic animals but reports that *P. antarctica* was the dominant or co-dominant substrate type for benthic animals in at least some portion of the 10 to 30 m depth range at 15 of 26 study transects in the relatively protected Ellis Fjord. Dhargalkar *et al.* (1988) also reported that *P. antarctica* dominated there and in a site of intermediate exposure but that *H. grandifolius* and *D. menziesii* dominated more exposed areas of the Vestfold Hills.

4. Temperature demands

Antarctic macroalgae are very well adapted to the low seawater temperatures of their environment. This applies especially to endemic Antarctic species such as the Antarctic members of the brown algal order Desmarestiales *Desmarestia anceps*, *D. antarctica*, *Himantothallus grandifolius*, *Phaeurus antarcticus* Skottsberg and the red algae *Myriogramme manginii*, *Pantoneura plocamioides* Kylin and *Phyllophora antarctica* (Table 2; Gómez *et al.* 2011). These species grow only up to 5 °C and exhibit upper survival temperatures (USTs) between 9 and 13°C. The red alga *Georgiella confluens* exhibits even lower temperature demands: It grows only at 0°C, but not at 5°C, and exhibits an UST of 11°C. In contrast, few endemic Antarctic species have higher temperature demands. The brown alga *Ascoseira mirabilis* grows up to 10°C but exhibits a low UST similar to the above mentioned species. The red algae *Gymnogongrus antarcticus* Skottsberg and *Phyllophora ahnfeltioides* Skottsberg, like *A. mirabilis*, grow up to temperatures of 10 or even 15°C, but exhibit considerably higher USTs of 19 or 22°C, respectively. So, the latter three species could theoretically occur even farther north, suggesting incomplete dispersal or incomplete collections. Alternatively, a reproduction boundary may limit their distribution to the Antarctic region (Bischoff-Bäsmann & Wiencke 1996).

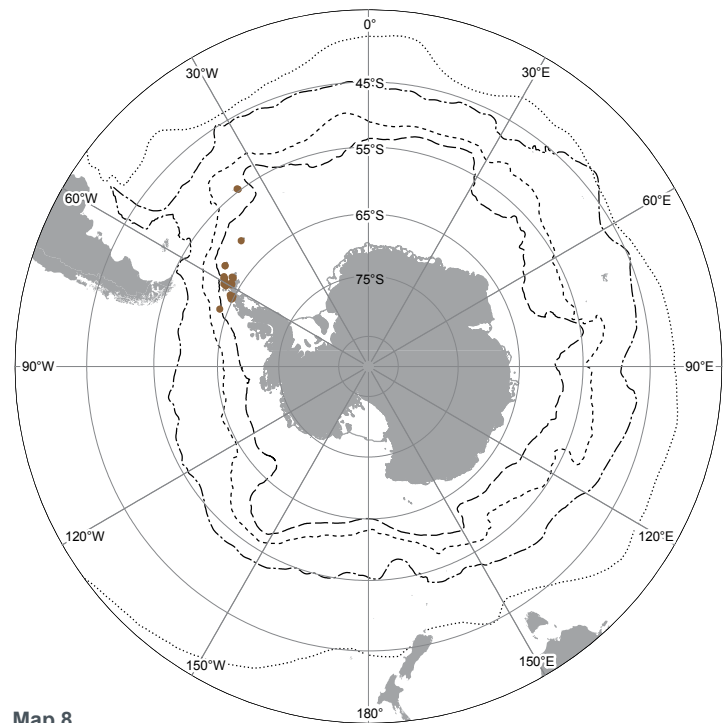
Antarctic-cold temperate brown and red algal species have higher temperature demands and typically grow up to 10(15)°C with USTs of 13–18°C (Table 2; Gómez *et al.* 2011). Some species, e.g. the Antarctic isolates of the red algae *Plocamium cartilagineum* and *Gigartina skottsbergii* Setchell & N.L. Gardner grow only at 0°C, but not at 5°C and exhibit USTs of 7 and 13–14°C. The Antarctic isolate of the red algae *Iridaea cordata* and *Ballia callitricha* (C.Agardh) Kützinger grow up to 5°C and exhibit USTs of 15–16 and 14°C, respectively. The temperature demands of the first three of these species indicate the existence of temperature ecotypes or even differentiation into separate species, as proposed by Hommersand *et al.* (2011). The same may apply also for *Ballia callitricha*. The Antarctic isolates tested show that these four species are limited northwards by their temperature-growth pattern to the Antarctic region.

The highest temperature demands of species from the Antarctic region were demonstrated in Antarctic cold-temperate green algae. These species grow up to 10, 15 or 20°C and exhibit USTs between 19 and 26(28)°C (Table



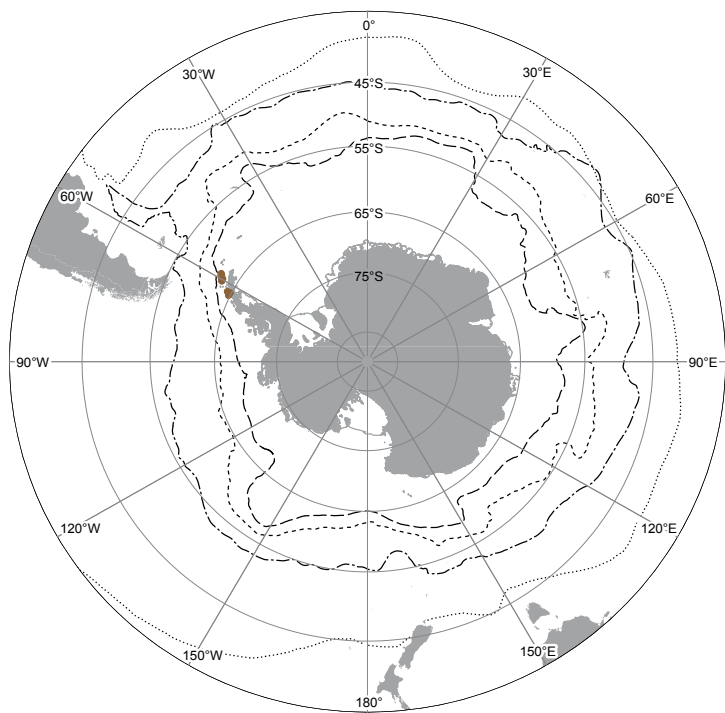
Map 7

● *Desmarestia anceps*



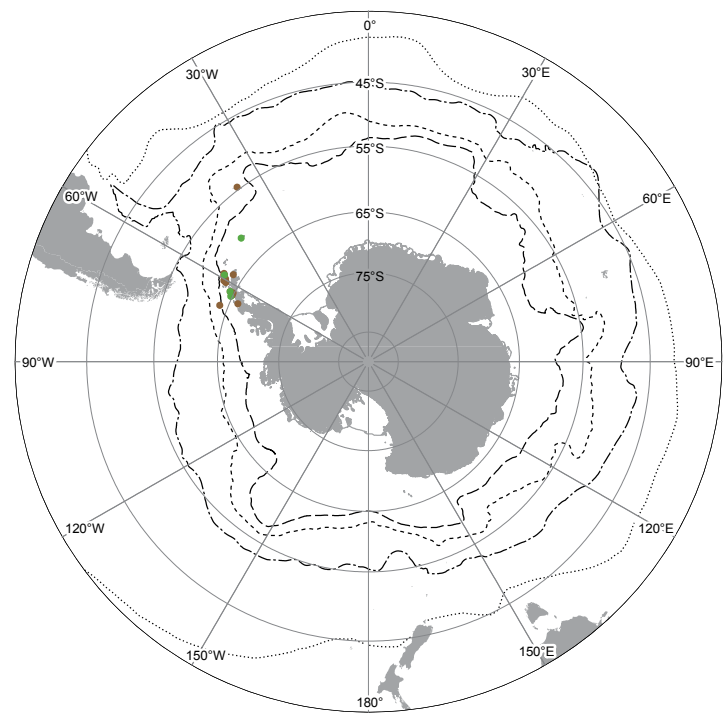
Map 8

● *Ascoseira mirabilis*



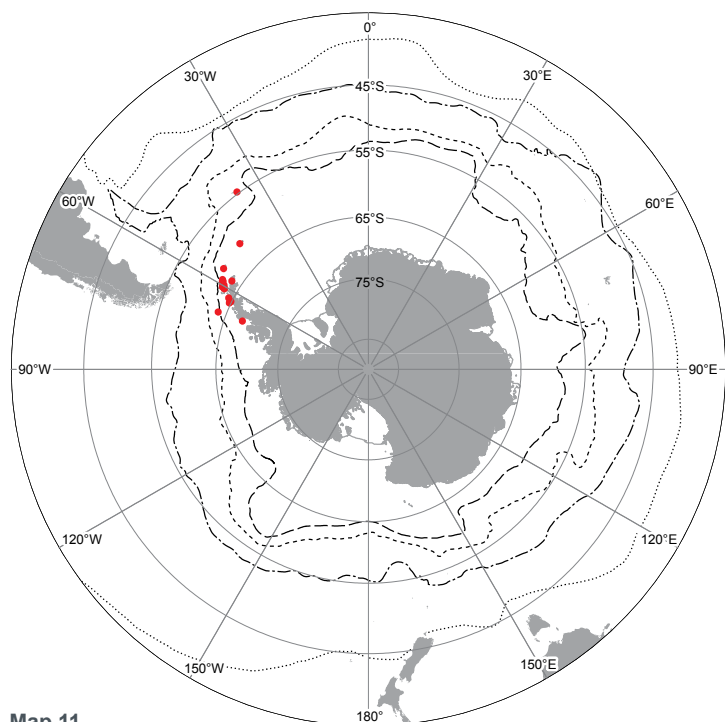
Map 9

● *Cystosphaera jacquinotii*



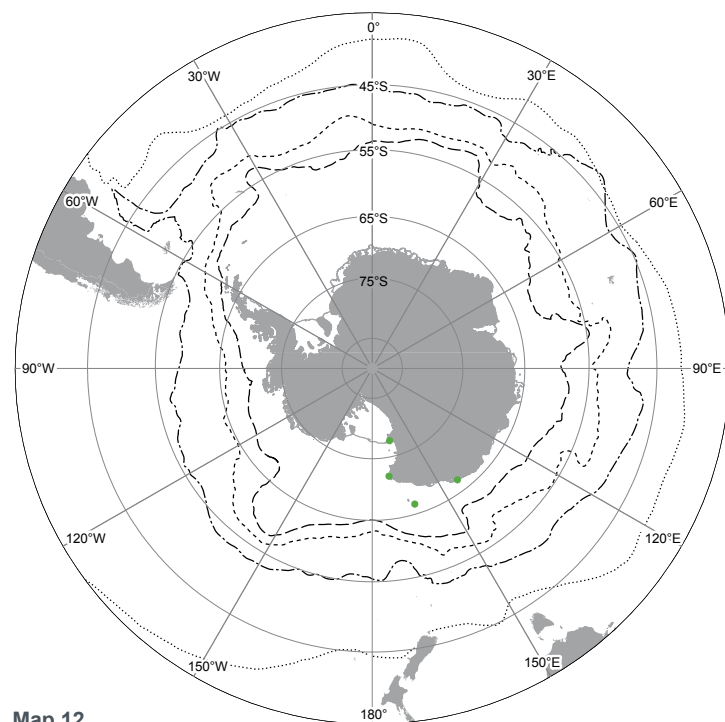
Map 10

● *Desmarestia antarctica*
● *Lambia antarctica*



Map 11

● *Myriogramme manginii*



Map 12

● *Chaetomorpha mawsonii*

Macroalgae Maps 7–11 Endemic Antarctic species occurring only in West Antarctica: Map 7. The brown alga *Desmarestia anceps*. Map 8. The brown alga *Ascoseira mirabilis*. Map 9. The brown alga *Cystosphaera jacquinotii*. Map 10. The brown alga *Desmarestia antarctica* (brown dots) and the green alga *Lambia antarctica* (green dots). Map 11. The red alga *Myriogramme manginii*. **Map 12.** The green alga *Chaetomorpha mawsonii*, an endemic Antarctic species occurring only in East Antarctica.

2; Gómez *et al.* 2011). These temperature requirements reflect the occurrence of these species on the shore in the supra- and eulittoral, where temperatures may rise to about 27 and 14°C, respectively (Zacher *et al.* 2011).

5. Geographic distribution

5.1. Endemic Antarctic species

Species with a circum-Antarctic distribution include *Himantothallus grandifolius* (Map 1), *Desmarestia menziesii* (Map 2), *Georgiella confluens* (Map 3), *Phycodrys antarctica* (Map 4), the red alga *Phyllophora antarctica* (Map 5) and the intertidal species *Porphyra endiviifolia* (Map 6). Species occurring in West Antarctica only are *Desmarestia anceps* (Map 7), *Ascoseira mirabilis* (Map 8), *Cystosphaera jacquinotii* (Map 9), *D. antarctica* (Map 10), *Myriogramme manginii* (Map 11) and *Lambia antarctica* (Skottsberg) Delépine (Map 10). *Chaetomorpha mawsonii* A.H.S. Lucas (Map 12) occurs in East Antarctica only.

The northern distribution of six of these species (*Desmarestia anceps*, *D. antarctica*, *Himantothallus grandifolius*, *Georgiella confluens*, *Myriogramme manginii*, *Phyllophora antarctica*) is limited by their temperature-growth pattern allowing growth only at temperatures at 5°C or below (Table 2). In the remaining seven species no or not sufficient data on the temperature requirements are available to explain their geographic distribution. As indicated above, their northern boundary may be determined by the temperature demands for reproduction in some cases.

The southern distribution boundaries of endemic Antarctic species are possibly determined by their inability to sustain the long periods under ice cover in almost total darkness or to withstand ice-abrasion. In species, whose reproduction is governed by photoperiod, e.g. in *Himantothallus grandifolius*, *Desmarestia anceps* and *D. menziesii* (Wiencke 1990, Wiencke & Clayton 1990, Wiencke *et al.* 1995, 1996), the southern distribution limit may also be determined by the daylength conditions at high latitudes. The southernmost location of *D. anceps*, for example, is at approx. 65°S (Map 7). At this latitude, fertility inducing daylengths of 5 to 7h occur for periods of about 6 weeks. At higher latitudes, this window is open for much shorter periods, too short for induction of fertility.

5.2. Antarctic-cold temperate species

Species extending from West Antarctica into the cold temperate region are *Adenocystis utricularis* (Map 13), *Gigartina skottsbergii* (Map 14) and *Porphyra plocamiestris* R.W. Ricker (Map 13). Species with a circum-Antarctic cold-temperate distribution include *Plocamium cartilagineum* (Map 15), *Monostroma hariatii* (Map 16), *Palmaria decipiens* (Map 17), *Iridaea cordata* (Map 18), and the intertidal species *Ulva hookeriana* (Map 18) and *Urospora penicilliformis* (Map 15).

Palmaria decipiens, *Iridaea cordata*, *Monostroma hariatii* and *Urospora penicilliformis* occur as far south as 77°S! The southernmost location of *Plocamium cartilagineum* is 74°S, 68°S in *Ulva hookeriana*, and 65–66°S in *Adenocystis utricularis*, *Gigartina skottsbergii* and *Porphyra plocamiestris*. These boundaries are certainly determined by the same characteristics as mentioned above for the endemic Antarctic species.

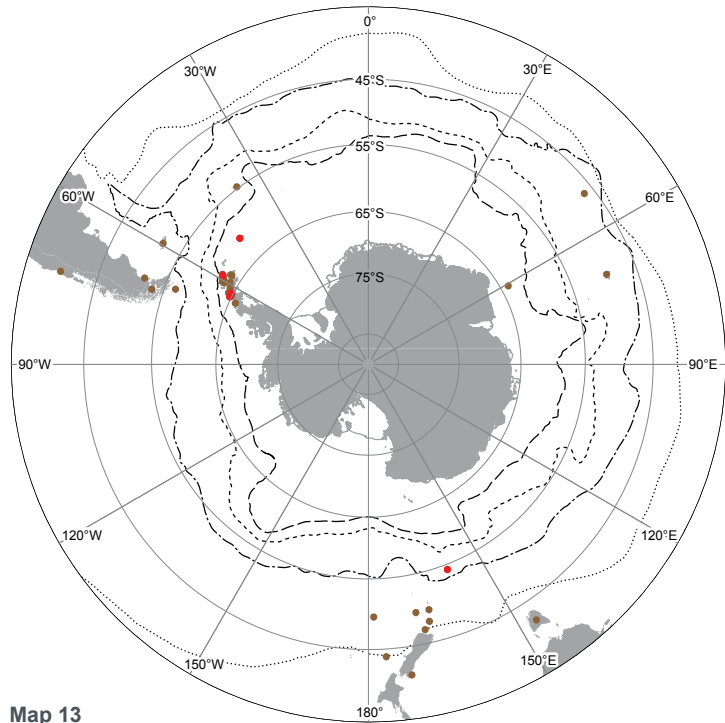
The northern distribution limit of *Palmaria decipiens* is probably a growth boundary located at the 4°C winter isotherm (Wiencke & tom Dieck 1989). Lethal boundaries seem to limit the Northern distribution of the supra- and eulittoral species *Adenocystis utricularis*, *Urospora penicilliformis* and *Ulva hookeriana* (Wiencke & tom Dieck 1990). The temperature requirements of *Monostroma hariatii*, *Porphyra plocamiestris* and the northern populations of *Iridaea cordata*, *Gigartina skottsbergii* and *Plocamium cartilagineum* have not been investigated so far. As indicated above, South American populations of these three species probably represent ecotypes or even different species according to molecular data (Hommersand *et al.* 2011).

6. Impact of global climate changes

Several studies were performed on the effect of UV radiation (UVR) on Antarctic macroalgae (Karsten *et al.* 2011), especially on their spores, which are the most UV-susceptible stages in their life history (Roleda *et al.* 2007, 2008, 2009, Zacher *et al.* 2007b, 2009). Therefore, enhanced UVR due to stratospheric ozone depletion may lead to changes in particular in depth distribution and during early succession (Zacher *et al.* 2007, Campana *et al.* 2011).

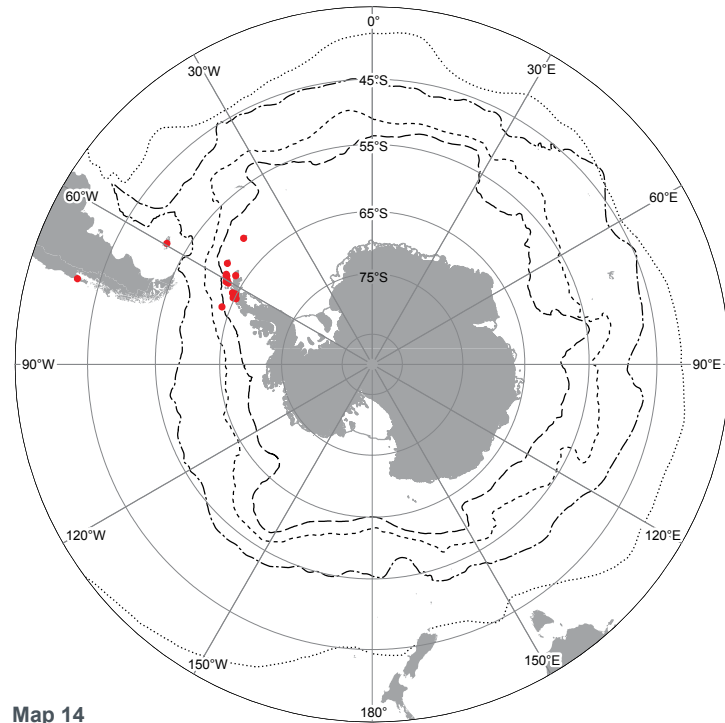
Table 2 Temperature requirements for growth and survival of endemic Antarctic species and species distributed in the Antarctic-cold temperate region (n.d.: no data; *: higher temperatures not tested; UST: Upper survival temperature).

Species	Growth range (°C)	UST (°C)	Reference
Endemic Antarctic species			
Phaeophyceae (brown algae)			
<i>Ascoseira mirabilis</i> Skottsberg	≤ 10	11	Wiencke & tom Dieck 1989
<i>Desmarestia anceps</i> Montagne	≤ 5	11-12	Wiencke & tom Dieck 1989
<i>Desmarestia antarctica</i> R.L.Moe & P.C.Silva	≤ 5	13	Wiencke & tom Dieck 1989
<i>Himantothallus grandifolius</i> (A.&E.Gepp) Zinova	≤ 5	11-13	Wiencke & tom Dieck 1989
<i>Phaeurus antarcticus</i> Skottsberg	≤ 5	11	Wiencke & tom Dieck 1989
Phaeophyceae (red algae)			
<i>Georgiella confluens</i> (Reinsch) Kylin	0	11	Bischoff-Bäsmann & Wiencke 1996
<i>Gymnogongrus antarcticus</i> Skottsberg	≤ 10 ≤ 10(15)	19 n.d.	Bischoff-Bäsmann & Wiencke 1996 Eggert & Wiencke 2000
<i>Myriogramme manginii</i> (Gain) Skottsberg	≤ 5	11	Bischoff-Bäsmann & Wiencke 1996
<i>Pantoneura plocamioides</i> Kylin	≤ 5	9	Bischoff-Bäsmann & Wiencke 1996
<i>Phyllophora ahnfeltioides</i> Skottsberg	≤ 10 ≤ 15	22 n.d.	Bischoff-Bäsmann & Wiencke 1996 Eggert & Wiencke 2000
<i>Phyllophora antarctica</i> A. & E.S.Gepp	≤ 5	12	Bischoff-Bäsmann & Wiencke 1996
<i>Phycodrys austrogeorgica</i> Skottsberg	n.d.	14	Bischoff-Bäsmann & Wiencke 1996
Antarctic-cold temperate species			
Phaeophyceae (brown algae)			
<i>Adenocystis utricularis</i> (Bory) Skottsberg	≤ 15	18	Wiencke & tom Dieck 1990
<i>Geminocarpus geminatus</i> (J.D.Hooker & Harvey) Skottsberg	≤ 10 ≤ 8	14-15 n.d.	Wiencke & tom Dieck 1990 McKamey & Amsler 2006
<i>Desmarestia confervoides</i> (Bory) M.Ramirez & A.Peters (cold-temperate isolate)	n.d.	25.8-26.4	Peters & Breeman 1992
Phaeophyceae (red algae)			
<i>Ballia callitricha</i> (C.Agardh) Kützing (Antarctic isolate)	≤ 5	14	Bischoff-Bäsmann & Wiencke 1996
<i>Delesseria lancifolia</i> J.Agardh	n.d.	16	Bischoff-Bäsmann & Wiencke 1996
<i>Gigartina skottsbergii</i> Setchell & N.L.Gardner (Antarctic isolate)	n.d. 0	13-14 13-14	Wiencke & tom Dieck 1990
<i>Iridaea cordata</i> (Turner) Bory (Antarctic isolate)	≤ 5	15-16	Wiencke & tom Dieck 1990
<i>Palmaria decipiens</i> (Reinsch) R.W.Ricker	≤ 10	16-17	Wiencke & tom Dieck 1989
<i>Plocamium cartilagineum</i> (Linnaeus) P.S.Dixon (Antarctic isolate)	0	7	Bischoff-Bäsmann & Wiencke 1996
<i>Rhodochorton purpureum</i> (Lightfoot) Rosenvinge	≤ 10	18	Bischoff-Bäsmann & Wiencke 1996
<i>Trematocarpus antarcticus</i> (Hariat) Fredericq & R.L.Moe	≤ 10	n.d.	Eggert & Wiencke 2000
Chlorophyta (green algae)			
<i>Acrosiphonia arcta</i> (Dillwyn) Gain	≤ 15	21-22	Wiencke & tom Dieck 1990
<i>Cladophora coelothrix</i> Kützing	≤ 12*	n.d.	McKamey & Amsler 2006
<i>Prasiola crispa</i> (Lightfoot) Kützing	≤ 20	24-28	Wiencke & tom Dieck 1990
<i>Ulothrix implexa</i> (Kützing) Kützing	≤ 20	25-26	Wiencke & tom Dieck 1990
<i>Ulothrix subflaccida</i> Wille	≤ 10	23-25	Wiencke & tom Dieck 1990
<i>Ulva hookeriana</i> (Kützing) Hayden, Blomster, Maggs, P.C., M.J.Stanhope & J.R.Waaland	≤ 20	25	Wiencke & tom Dieck 1990
<i>Urospora penicilliformis</i> (Roth) Areschoug	≤ 15	19	Wiencke & tom Dieck 1990



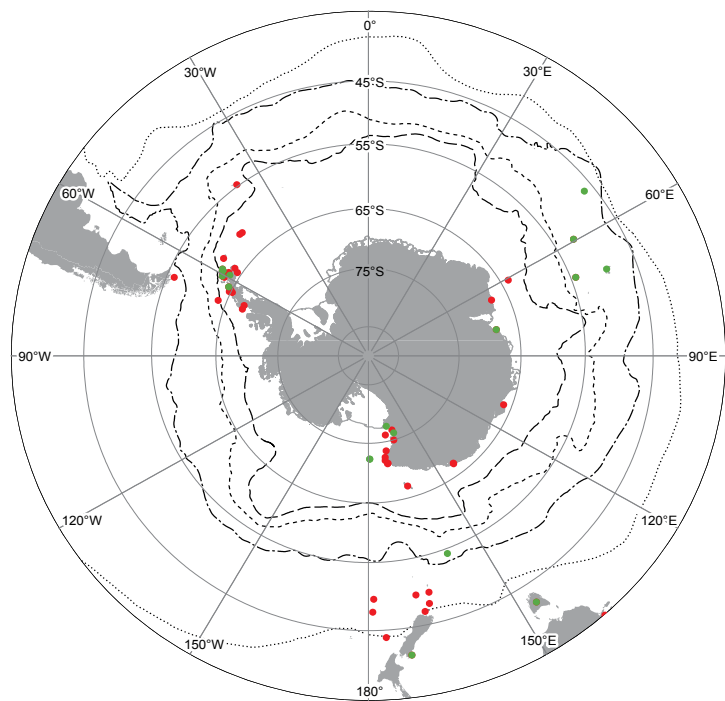
Map 13

● *Adenocystis utricularis*
● *Porphyra plocamiestris*



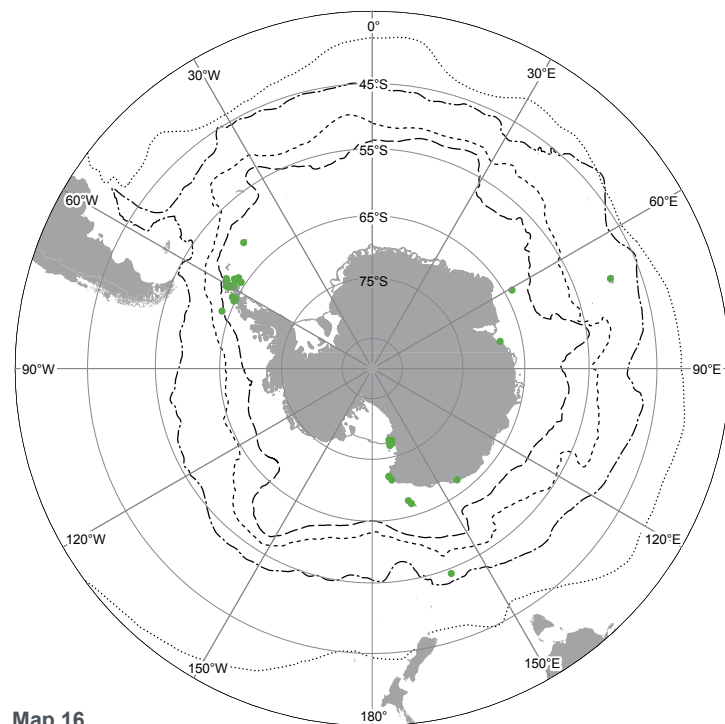
Map 14

● *Gigartina skottsbergii*



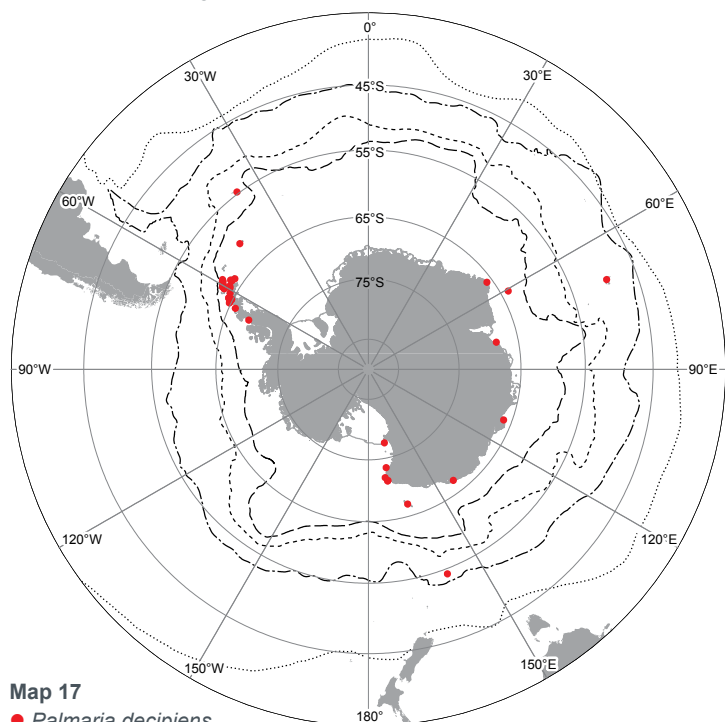
Map 15

● *Urospora penicilliformis*
● *Plocamium cartilagineum*



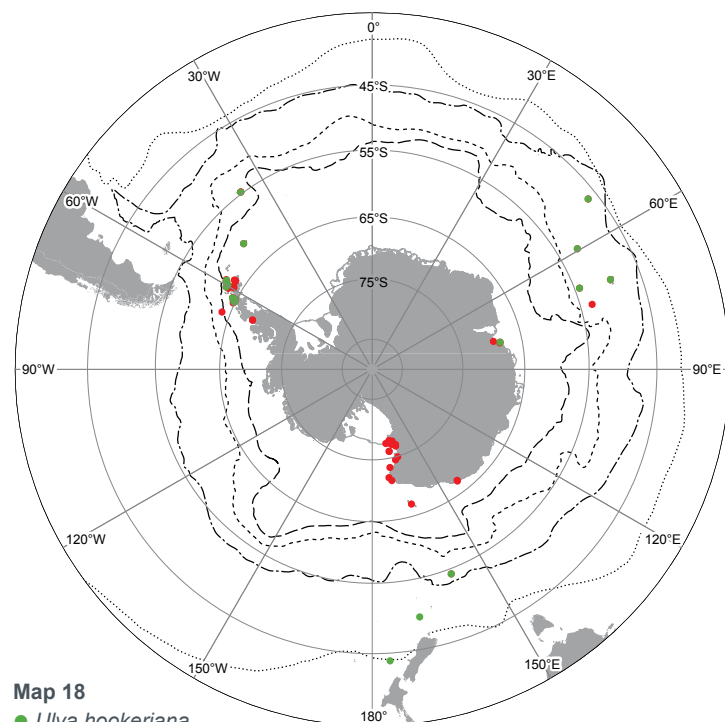
Map 16

● *Monostroma hariotii*



Map 17

● *Palmaria decipiens*



Map 18

● *Ulva hookeriana*
● *Iridaea cordata*

Macroalgae Maps 13–14 West-Antarctic - cold-temperate species: Map 13. The brown alga *Adenocystis utricularis* (brown dots) and the red alga *Porphyra plocamiestris* (red dots). Map 14. The red alga *Gigartina skottsbergii* (red dots). **Maps 15–18.** Circum-Antarctic - cold-temperate species: Map 15. The green alga *Urospora penicilliformis* (green dots) and the red alga *Plocamium cartilagineum* (red dots). Map 16. The green alga *Monostroma hariotii*. Map 17. The red alga *Palmaria decipiens* (red dots). Map 18. The green alga *Ulva hookeriana* (formerly *Enteromorpha bulbosa*; green dots) and the red alga *Iridaea cordata* (red dots).

As explained above, temperature is one of the most important factors controlling biogeographic distribution of macroalgae. Therefore, shifts in their distribution are inevitable during periods of changing temperatures as demonstrated in the geological past e.g. during the last glaciation. At this time, Antarctic species were able to extend their distribution towards the tropics. *Desmarestia viridis* (O.F. Müller) J.V. Lamouroux / *confervoides* (Bory) M. Ramirez & A. Peters and *Acrosiphonia arcta* (Dillwyn) Gain even crossed the equator when tropical water temperatures were just low enough to allow passage of the hardest life history stage through the tropics (Peters & Breeman 1992; van Oppen *et al.* 1993; Bischoff & Wiencke 1995).

Similar changes may be provoked during the present period of global warming. Modeled temperature changes through the end of 21st century indicate that many Antarctic macroalgae will, however, probably not strongly alter latitudinal distributions (Müller *et al.* 2011). But, beside the direct effect of temperature on geographic distribution, there may be indirect effects mediated by milder and shorter periods of sea ice cover, particularly along the southern portion of the western Antarctic Peninsula (Smith & Stammerjohn 2001, Stammerjohn *et al.* 2008). Such changes are thought to exert a significant impact on marine communities (Clarke *et al.* 2007, Ducklow *et al.* 2007, McClintock *et al.* 2008). Therefore, macroalgal communities will presumably expand southward due to less strong ice abrasion and improved light conditions, and new ice-free areas appearing due to glacier retreat will be colonised by seaweeds. Beside changes in geographic distribution global warming may also result in changes in zonation patterns. as increasing inflow of turbid meltwater during summer will reduce the light penetration into the water and, hence, elevate the lower depth distribution limits of seaweeds.

Antarctica will not only be affected by stratospheric ozone depletion and global warming, but will certainly also be threatened by ocean acidification as a result of human use of fossil fuels. When CO₂ enters the ocean surface, pH and carbon ion concentrations will decrease, in contrast, CO₂ and bicarbonate concentrations will increase (Fealy *et al.* 2004). As the solubility of gases is higher in colder waters, especially polar regions will be strongly affected. Elevated CO₂ levels may support photosynthesis (Gordillo *et al.* 2003), but calcification of calcareous algae will be impaired (Leclerc *et al.* 2000, McClintock *et al.* 2009). Further studies are needed here. In this respect, special attention has to be paid to the juvenile developmental stages of seaweeds and their performance under elevated CO₂ levels as these stages are the most susceptible to environmental perturbations as exemplified for UV radiation and temperature (Müller *et al.* 2008, Roleda *et al.* 2007, 2008, Zacher *et al.* 2007a, 2007b).

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope

Biogeographic information is of fundamental importance for discovering marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future distributions, monitoring biodiversity, or supporting conservation and sustainable management strategies.

The recent extensive exploration and assessment of biodiversity by the Census of Antarctic Marine Life (CAML), and the intense compilation and validation efforts of Southern Ocean biogeographic data by the SCAR Marine Biodiversity Information Network (SCAR-MarBIN / OBIS) provided a unique opportunity to assess and synthesise the current knowledge on Southern Ocean biogeography.

The scope of the Biogeographic Atlas of the Southern Ocean is to present a concise synopsis of the present state of knowledge of the distributional patterns of the major benthic and pelagic taxa and of the key communities, in the light of biotic and abiotic factors operating within an evolutionary framework. Each chapter has been written by the most pertinent experts in their field, relying on vastly improved occurrence datasets from recent decades, as well as on new insights provided by molecular and phylogeographic approaches, and new methods of analysis, visualisation, modelling and prediction of biogeographic distributions.

A dynamic online version of the Biogeographic Atlas will be hosted on www.biodiversity.aq.

The Census of Antarctic Marine Life (CAML)

CAML (www.caml.aq) was a 5-year project that aimed at assessing the nature, distribution and abundance of all living organisms of the Southern Ocean. In this time of environmental change, CAML provided a comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. CAML was initiated in 2005 as the regional Antarctic project of the worldwide programme Census of Marine Life (2000-2010) and was the most important biology project of the International Polar Year 2007-2009.

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS, www.iobis.org), under the aegis of SCAR (Scientific Committee on Antarctic Research, www.scar.org). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with biodiversity.aq provided free access to more than 2.9 million Antarctic georeferenced biodiversity data, which allowed more than 60 million downloads.

The Editorial Team



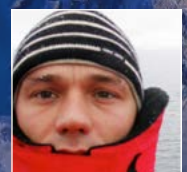
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