

Research Article

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Vertical distribution of brown and red macroalgae along the central Western Antarctic Peninsula

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Abstract: Fleishy macroalgae dominate the hard bottom, shallow waters along the Western Antarctic Peninsula (WAP). Although there are numerous reports on their ecology, geographic distribution, and to a lesser extent, vertical (depth) distribution in the northern portions of the WAP, much less is known farther south along the central portion of the WAP. Here we provide the first report of the vertical distributions of brown and red fleishy macroalgae in this region based on scuba-derived collections at 14 study sites between southern Anvers Island (64.8°S, 64.4°W) in the north and central Marguerite Bay (68.7°S, 67.5°W) in the south. Although several overstory brown macroalgal species that can be common along the northern WAP including *Desmarestia anceps* and *Cystosphaera jacquinotii* are mostly absent from the central WAP, the vertical distributions of the brown macroalgae *Desmarestia menziesii* and *Himantothallus grandifolius* are similar to the northern WAP even though their percent cover is much lower. Likewise, the vertical distribution of the 14 most widespread red

macroalgae, where they occur, mirrored those known from the northern part of the WAP even though macroalgal cover, biomass, and total species richness declined markedly to the south across this region due to increasing sea ice concentrations.

Keywords: depth distribution; Phaeophyceae; polar; Rhodophyceae; seaweeds

1 Introduction

The macroalgal flora of Antarctica consists of over 150 currently known species, which is likely a substantial underestimate of the actual species richness (Oliveira et al. 2020). Macroalgae are distributed throughout the entire coastline of the continent including a few species as far south as southern McMurdo Sound, which is as far south globally as open water ever occurs (Wiencke and Amsler 2012; Wiencke et al. 2014). However, many, probably most, of the known species are only found along the western side of the continental Antarctic Peninsula and the islands to its west and north (Oliveira et al. 2020; Wiencke and Clayton 2002; Wiencke et al. 2014). As commonly done, herein we refer to this entire region as the Western Antarctic Peninsula (WAP).

The vast majority of published reports on the WAP flora come from observations between the South Orkney Islands in the northeast and Anvers Island in the southwest (Figure 1), which for convenience we hereafter call the “northern WAP.” General descriptions of macroalgal distribution and ecology in the northern WAP date back to 1906 with at least 35 published reports since 1965 (see Amsler et al. 2023, Appendix 1) in addition to numerous other reports comprised mainly of species lists. Farther south, waters near Rothera Station on Adelaide Island (Figure 1) are relatively well studied (e.g., Rozema et al. 2017; Venables et al. 2023) but there are only limited reports of macroalgal diversity or abundance (Barnes and Brockington 2003; Bowden 2005; Mystikou et al. 2014). From these few reports it is evident that the Rothera area has many fewer macroalgal species with lower macroalgal cover and biomass than commonly

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reported in the northern WAP. Unfortunately, until recently, the only other published information on the flora along the WAP south of Anvers Island were species lists and casual observations from the early 1970s (DeLaca and Lipps 1976; Moe and DeLaca 1976) at nine sites extending as far south as Marguerite Bay (Figure 1). For convenience in this article, we refer to this area south of Anvers Island as the “central WAP.”

In 2019, we participated in a research cruise using scuba diving to make by-hand collections of macroalgae and macroinvertebrates and to record video transects of the benthos at four study sites off southern Anvers Island and 10 additional sites located in the central WAP. Fleishy macroalgal cover was strongly, negatively correlated with annual sea ice concentration while overall community diversity was positively correlated with fleshy macroalgal cover (Amsler et al. 2023). Macroalgal stable isotope values varied little across the latitudinal and sea ice range but, across the overall communities, food web length and trophic niche width were negatively correlated with sea ice cover (Iken et al. 2023). Although Amsler et al. (2023) present species lists for each site as well as macroalgal cover both overall and by depth at each site by macroalgal group, describing the vertical (depth) distribution of individual macroalgal species was beyond the scope of that report. Nonetheless, information on the vertical distributions of macroalgae, particularly red macroalgae, have been completely lacking from the central WAP. This contribution fills that information gap for the overstory brown and most widespread red macroalgal species, which will be important for making predictions about how benthic communities in the central WAP will be impacted by climate change (e.g., Amsler et al. 2023; Deregis et al. 2023).

2 Materials and methods

Fourteen study sites (Figure 1) between the Joubin Islands off southwest Anvers Island (64.8°S, 64.4°W) in the north and the Terra Firma Islands in Marguerite Bay (68.7°S, 67.5°W) in the south were sampled in April and May 2019. The sites were selected because they spanned the range of satellite-determined sea ice concentrations in this region and because they were within a defined window of satellite-determined open water turbidity. Further information on site selection parameters, coordinates, sea ice concentrations, and turbidity levels are detailed in Amsler et al. (2023). Sea ice concentration data presented herein were derived from weekly National Ice Center charts (Dedrick et al. 2001; Fetterer 2006) averaged over the entire five year period preceding sampling (1 April 2014 through 1 April 2019).

Sites were designated by letters from north (A) to south (N) (Figure 1). At each site, vertical transects were surveyed by scuba divers. Where bottom topography allowed, transects began at 40 m depth and ended at 5 m depth. All sites contained transects that covered the 20–5 m

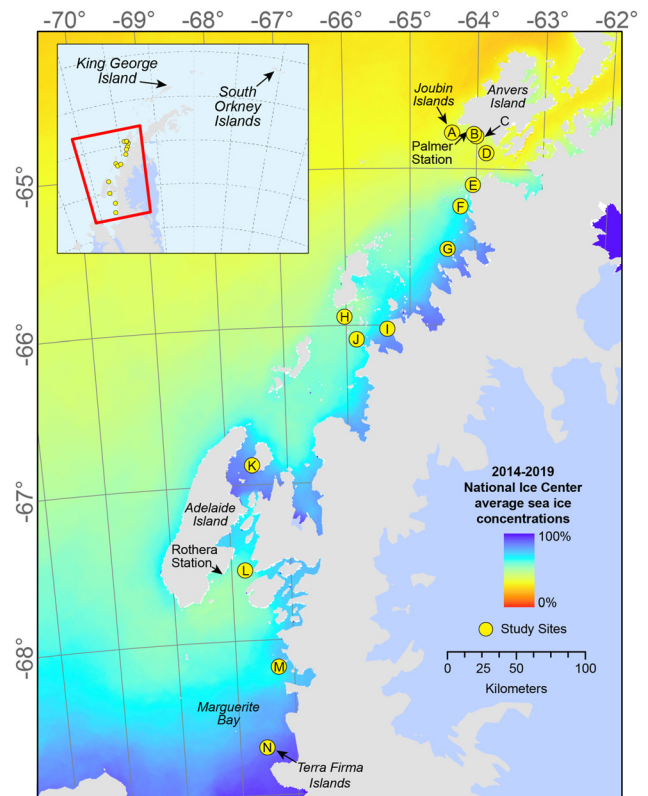


Figure 1: Study sites along the central Western Antarctic Peninsula. Inset shows the entire northern and central portions of the Antarctic Peninsula. The 14 research sites, designated north to south as A through N, were surveyed between April 23 and May 18, 2019. Their locations spanned the range of annual sea ice coverage (color scale bar). Modified from Amsler et al. (2023).

depth range, and 11 of the sites had transects starting at least at 30 m depth. At each 5 m depth interval between 35 and 5 m depth the transect included a 5 m long horizontal component (cf. Amsler et al. 2023) along which one of each macroalgal species observed was sampled and placed into an individually labeled bag for later identification. Macroalgae were identified, in most cases to species level, upon their return to the research ship. At least one pressed voucher specimen of each species at each site was prepared. Upon return to the United States, the voucher material was compared to previously identified herbarium specimens and to each other across sites to confirm identifications and ensure consistency of identifications across the study sites. Voucher macroalgae are archived in the macroalgal herbarium of C. Amsler at the University of Alabama at Birmingham. Only macroalgae that were attached to the substratum were included; unattached, drift macroalgae were not collected to ensure that only macroalgae growing at that depth were included in the dataset. Three parallel vertical transects spaced approximately 100 m apart were surveyed at all sites except for site I where a logistical issue limited us to two transects. At sites F, H, and M, bottom topography prevented one of the three transects from beginning as deep as the others, as also occurred in two of the transects at site N. At site J, the sample bag from 10 m depth on one transect was lost. After the transects at each site were completed, with the exception of site I, an additional scuba dive was made to collect macroalgal species that were present at the site but not collected along the horizontal components of the transects.

As a semi-quantitative representation of the vertical distribution of macroalgae across the geographic range of our samples, we tabulated the number of transects at each depth at each site where a species was present. This was done for five brown algal species that comprise the overstory canopy as well as for the 14 (of 27 total) understory red algal species that were collected at five or more sites (Amsler et al. 2023). Amsler et al. (2023) reported *Pantoneura plocamioides* from nine sites due to a data transcription mistake. The correct number of sites is five as reported here. *Iridaea 'cordata'* is reported with the specific epithet in single quotes because this entity on the WAP is genetically distinct from the type locality of *I. cordata* in South America and almost certainly represents a different but heretofore unnamed species (Hommersand et al. 2009; Ocaranza-Barrera et al. 2019). *Myriogramme smithii* is reported in single quotes because algae identified as this species in Antarctica probably represent a new species of *Hymenena* (Hommersand et al. 2009). *Hymenocladopsis* spp. are reported as such because the number and identity of Antarctic species in this genus is unclear (Hommersand et al. 2009). Our collections of *Hymenocladopsis* probably represent a single species but we cannot be certain. *Plocamium* sp. is reported as such because it is genetically distinct from all described *Plocamium* spp. elsewhere in the world (Dubrasquet et al. 2018; Hommersand et al. 2009) but has not yet been formally described as a new species. All species names used and the taxonomic authorities for them are those currently accepted in AlgaeBase (Guiry and Guiry 2023).

In addition to algal collections, each transect was video recorded at 4K resolution using a Paralenz DC+ underwater cameras and two Light and Motion Sola 3800 video lights. A custom-built mount held two Z-Bolt SCUBA-BL low temperature blue laser pointers 10 cm apart to provide scaling for video analyses. Video stream processing of transects was accomplished with VLC software (VideoLAN Organization) and Coral Point Count with Excel extensions (CPCe 4.1; National Coral Reef Institute at Nova Southeastern University; Kohler and Gill 2006). The data were compiled using the automatic Excel spreadsheet generation feature of CPCe (Kohler and Gill 2006) to yield percent cover data as described in detail by Amsler et al. (2023). Camera malfunctions resulted in the loss of video from one transect each at sites H and K.

Red macroalgae often could not be confidently identified to species in the recordings and therefore we are not able to report percent cover data for them. With the exception of *Desmarestia menziesii* and *D. anceps*, which could only be distinguished from each other if a holdfast was in clear view, the other overstory brown algae (*Himantothallus grandifolius*, *D. antarctica*, and *Cystosphaera jacquinotii*) could be confidently identified to species. Unlike the by-hand collections, drift macroalgae usually could not be clearly distinguished from attached algae in the video analyses so the percent cover data probably include some unattached macroalgae.

Graphs of the data (Figures 2–5) were prepared using Microsoft Excel and PowerPoint. Figure 1 was prepared with ArcGIS 2.X, ArcGIS 3.X, and Adobe Illustrator.

3 Results

The total number of species in each group collected at each site is presented in Table 1. The single green algal species present at any site was *Lambia antarctica*. *Desmarestia menziesii* was the most widespread species (Figure 2). It was

present at all sites except site K where no fleshy macroalgae at all were present. *Desmarestia menziesii* was not observed on any of the transects at site D but was found on the subsequent general collection dive. It was most commonly present in the shallower transects and was usually the only brown alga collected at 5 m depth (Figure 2). *D. anceps* was only collected at three sites (Figure 2). It was observed between 5 and 25 or 30 m at sites A and B but only at a single depth (15 m) on one transect at site G. As noted above, *D. menziesii* and *D. anceps* could only rarely be confidently separated in the video transects but except for sites A, B, and 15 m depth at site G, the percent cover data for the two species combined (Figure 3) should represent only *D. menziesii*. The vertical distribution by percent cover of *D. menziesii* and *D. anceps* combined was usually similar in terms of the number of transects at which it was collected by hand, but this was not always true, for example at site L where it was only collected by hand at 5 m but was only present in the video data between 10 and 30 m (Figures 2 and 3).

Himantothallus grandifolius had the widest distribution across depths of the brown algae in terms of both presence-absence in transects (Figure 2) and percent cover (Figure 3) although it was never observed at 5 m depth. *Cystosphaera jacquinotii* was only observed at 20 m and deeper in the four northernmost sites (A through D; Figure 2). However, its percent cover was usually low where it was observed, with a maximum cover of 13.3 % at the single depth (30 m) and transect where it occurred at site C. *Desmarestia antarctica* was present across depths, albeit not at every single depth, in four of the six sites where it occurred in the presence-absence, by-hand collections (Figure 2). However, its percent cover only exceeded 4 % at 5 m depth at sites B and C (10.3 ± 6.2 and 21.0 ± 5.4 , means \pm standard error, respectively).

Red macroalgae were found at all sites except K, although at site N the only red macroalgal species was *Phyllophora antarctica*, for which data are not included herein as it was only present at three sites total (Amsler et al. 2023). *Iridaea 'cordata'* was present at all other sites except for site L (Figure 4). It was most commonly observed at 5 m depth but at some sites was found as deep as 35 m (Figure 4). *Plocamium* sp. was present across most or all of the depth range at all sites where it occurred (Figure 4). A similar pattern with sometimes a bias towards shallower depths was observed in *Sarcopeltis antarcticus* and *Trematocarpus antarcticus*, and sometimes with a bias towards deeper depths in *Myriogramme manginii* (Figure 4). The seven species presented in Figure 5 were most commonly found at deeper depths but some ranged shallower, particularly at the three highest ice cover sites (M, G, and I; Figure 5).

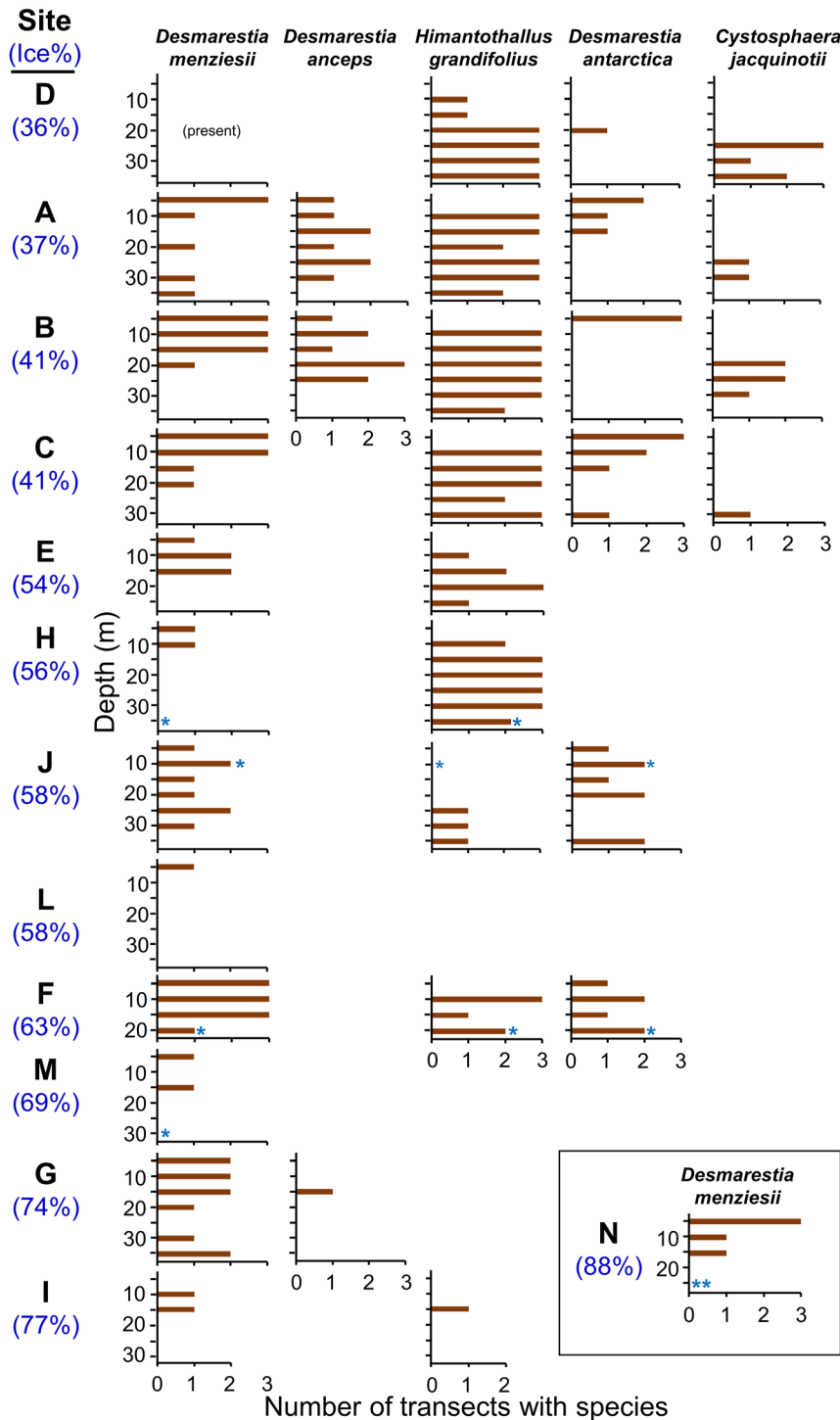


Figure 2: Vertical distribution of brown macroalgal species by the number of transects in which they were present in the diver by-hand collections. Sites are ordered by National Ice Center average sea ice concentrations from 2014 to 2019. No fleshy macroalgae were present at site K so it is not included. Only two transects were sampled at site I, so the abscissa only extends to two for that site. Single blue asterisks indicate one less transect collection at that depth at that site, two asterisks indicate two less; “(present)” indicates that the species was found in general collections at the site but was not present in the transect collections.

4 Discussion

Compared to the many reports of brown macroalgal distribution along the northern WAP (reviewed by Wiencke et al. 2014), it is perhaps surprising that at sites (except site J) where *Himantothallus grandifolius* occurred it was always the dominant overstory brown alga below 5 m depth in

terms of percent cover. In the northern WAP it is common for *Desmarestia anceps* to dominate in terms of cover and biomass at intermediate depths, often between *D. menziesii* dominating in shallower water and *H. grandifolius* below (e.g., Brouwer et al. 1995; Klöser et al. 1996; Quartino et al. 2001; Valdivia et al. 2015). However, *D. anceps* is not found at all sites in the region where other *Desmarestia* spp. or

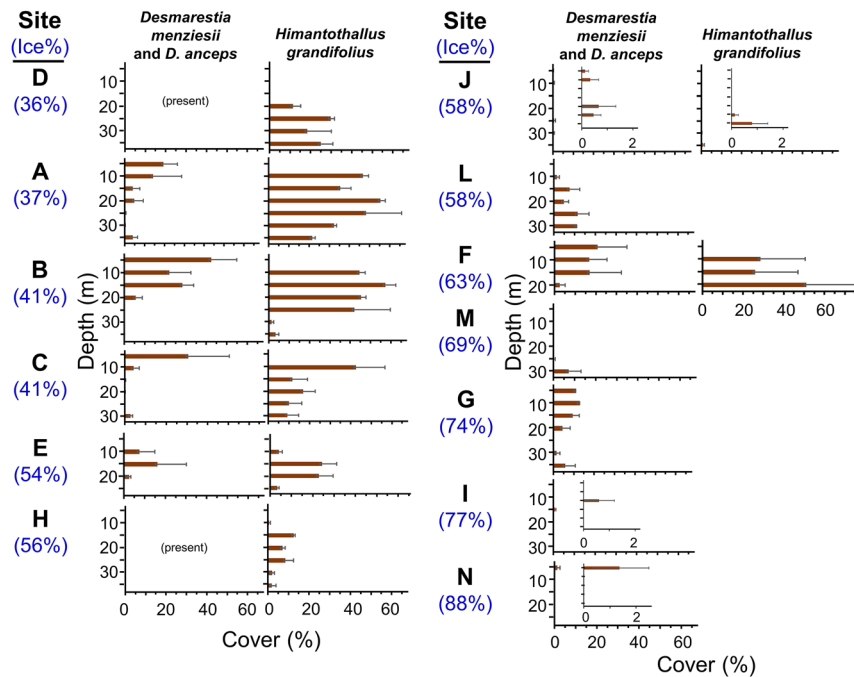


Figure 3: Vertical distribution of *Desmarestia menziesii* and *Desmarestia anceps* combined and of *Himantothallus grandifolius* at horizontal depth intervals from video transect analyses. Means + standard error of mean. Sample size was two at sites H, I, and K and three at all other sites. Sites are ordered by National Ice Center average sea ice concentrations from 2014 to 2019. No fleshy macroalgae were present at site K so it is not included. “(present)” indicates that the species was found in general collections at the site but was not present under a random dot in the video analyses.

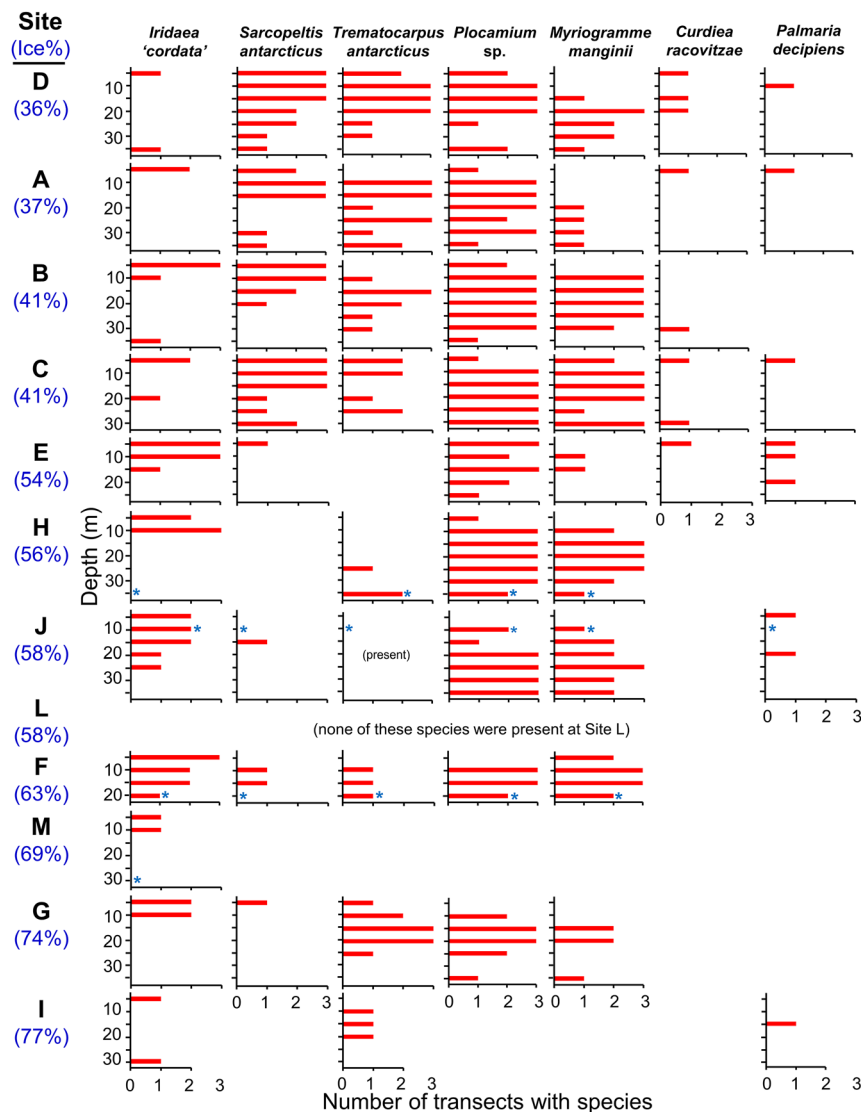


Figure 4: Vertical distribution of seven red macroalgal species by the number of transects in which they were present in the diver by-hand collections. Sites are ordered by National Ice Center average sea ice concentrations from 2014 to 2019. No fleshy red macroalgae were present at site K, and none of the species included in this report were present at site N. Only two transects were sampled at site I, so the abscissa only extends to two for that site. Single blue asterisks indicate one less transect collection at that depth at that site; “(present)” indicates that the species was found in general collections at the site but was not present in the transect collections.

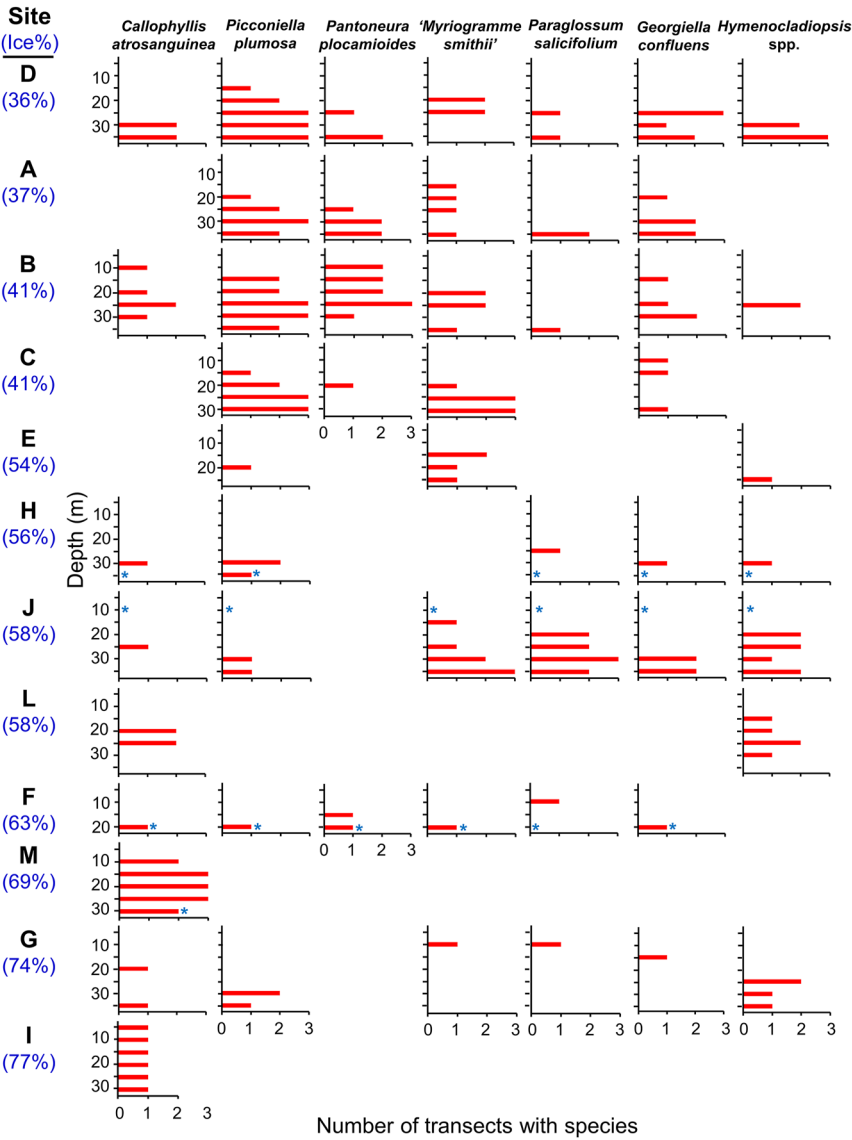


Figure 5: Vertical distribution of seven additional red macroalgal species by the number of transects in which they were present in the diver by-hand collections. Other details as in Figure 4.

Table 1: Number of macroalgal species found at each site by group.

Site	Fleshy macroalgal species			
	Brown	Red	Green	Total
A	5	17	1	23
B	7	18	1	26
C	4	12	1	17
D	4	15	0	19
E	2	13	0	15
F	4	16	1	21
G	2	16	1	19
H	2	10	1	13
I	2	5	0	7
J	3	14	0	17
K	0	0	0	0
L	1	3	0	4
M	2	2	0	4
N	1	1	0	2

H. grandifolius occur (e.g., Moe and DeLaca 1976; Pellizzari et al. 2017, 2023; Valdivia et al. 2015). Our (CDA, MOA, SH, and KI) personal observations from well over 1500 dives in the vicinity of sites A through D (particularly near B and C) since 1985, including semi-quantitative observations presented in Heiser et al. (2023; Table S2), are that while *D. anceps* is often the dominant overstory macroalga between 5–10 and 30 m or sometimes deeper, it is not uncommon for it to be absent at some sites or to have only limited cover as in the present dataset. As discussed in more detail in Amsler et al. (2023), our observation of *D. anceps* at a single depth on a single transect at site G is the only credible report of it south of 65°S latitude, a range limitation probably resulting from day-length requirements for reproduction in its microscopic gametophyte phase (Wiencke et al. 1996). Although Klöser et al. (1994) hypothesized that *D. menziesii* and *D. anceps* could competitively exclude *H. grandifolius* except at

greater depths at King George Island (Figure 1), our data do not support that conclusion in the central WAP. *Desmarestia menziesii* was found throughout the depth range sampled in by-hand collections at many of the sites but, where present, *H. grandifolius* dominated in the intermediate depth range often dominated by *D. anceps* in the northern WAP. Culture studies of gametophytes of the other members of the Desmarestiaceae that we observed indicate that the daylength requirements of their gametophytes should not limit their geographic distribution as is the case with *D. anceps* (Matula et al. 2022; Wiencke and Clayton 1990; Wiencke et al. 1991, 1995).

As also discussed in Amsler et al. (2023), the lack of brown macroalgae at site D above 20 m in the percent cover data and at 5 m in the by-hand collections is probably due to iceberg scouring long enough prior to our 2019 collections to allow presumably shorter-lived red macroalgae to recolonize but not longer-lived overstory brown macroalgae. Site D is in the Wauwermans Island group and, at another location in the island group in a previous study, we observed a high cover of *D. menziesii*, *D. anceps*, and *H. grandifolius* throughout the 5–29 m depth range where observations were recorded (Heiser et al. 2023; Table S2). Ice scour probably also explains the discrepancy in our data at site L where *D. menziesii* was present only at 5 m in by-hand collections but only between 10 and 30 m in the percent cover data. As noted in Section 2, only macroalgae attached to substrata were collected by hand but the video analysis could not reliably distinguish attached versus unattached, drift algae. The *D. menziesii* observed in the video analysis at site L were likely individuals that had been dislodged from the substratum by ice scour. The sea urchin *Sterechinus neumayeri* was particularly abundant at site L, although not at 5–10 m (Amsler et al. 2023), and commonly covers itself with drift macroalgae (e.g., Amsler et al. 1999). Diver observations at the site recorded in our field notes indicated that many, and on one transect, all, of the macroalgae observed were attached to urchins rather than the substratum. The vertical distribution of macroinvertebrates at site L also suggests the impacts of ice scour at shallow depths (Amsler et al. 2023). A similar difference between by-hand and percent cover patterns occurs at site M, which had the second highest cover of *S. neumayeri*.

We are aware of only few reports of the vertical distribution of red macroalgae anywhere along the northern WAP, and many specifically report only on a subset of the red macroalgal species presumably present with others lumped into one or more groups or not reported at all. The only quantitative reports deeper than 25 m are those of DeLaca and Lipps (1976) to 31 m at one site on Anvers Island (Figure 1), Brouwer et al. (1995) to 29 m at one site on Signy Island in the South Orkney Islands (Figure 1), Klöser et al.

(1996) to approximately 35 m from 14 transects in Potter Cove on King George Island (Figure 1), and Valdivia et al. (2015) to 30 m at six sites in Fildes Bay on King George Island. Klöser et al. (1996) report the vertical distribution of most red macroalgae in species groups rather than individually. Valdivia et al. (2015) only report on one red macroalga in the main text but an additional 18 are included in supplementary material, including at least 12 of the species included here (they report “*Delesseria* sp.” at one site that could be *Paraglossum salicifolium* but only at 5–10 m depth, which in our personal experience from Anvers Island is more likely to have been *P. amsleri*). Otherwise, the only studies we are aware of that provide vertical distribution data for more than approximately five individual red macroalgal species are: 1) DeLaca and Lipps (1976), reporting 19 species of which 10 are reported on herein; 2) Amsler et al. (1995), also at Anvers Island, reporting 17 species of which 12 are included herein; and 3) Ko et al. (2020, mostly in Supplementary information 5) reporting 18 species from six sites in Maxwell Bay on King George Island, of which 12 species are included here. Ko et al. (2020) built on an earlier study at the same sites that reported general vertical distributions qualitatively (Chung et al. 1994).

We chose to only include red macroalgal species in this report that were collected from at least five sites, which as noted previously excluded an additional 13 red algal species reported by Amsler et al. (2023). Most of these 13 species are included in the other studies listed in the previous paragraph. We did not include them here because most were present in only one or two transects or depths in the central WAP sites (if found in the central WAP sites at all) and so are of limited utility in generalizing about vertical distributions. The by-hand collection data for these additional 13 red macroalgal species are available at the United States Antarctic Program Data Center as noted in the Data Accessibility Statement, below.

The vertical distributions of red macroalgal species we observed were usually similar across sites and were generally similar to the distributions observed in previous studies in the northern WAP. *Plocamium* sp. and *Myriogramme manginii* had consistently the widest vertical distributions at sites where they occurred. Both species were also reported across depths in previous Anvers Island reports (Amsler et al. 1995; DeLaca and Lipps 1976), as was reported for *Plocamium* sp. from four studies at King George Island (Klöser et al. 1996; Ko et al. 2020; Quartino et al. 2001; Valdivia et al. 2015) and one on Signy Island (Brouwer et al. 1995). *M. mangini* was also reported in species groups found across depths by Klöser et al. (1996) as well as, but only rarely, across depths as an individual species by Ko et al. (2020) and Valdivia et al. (2015). Previous reports of the most geographically widespread red

macroalga in our study, *Iridaea 'cordata'*, usually have it restricted to 5–10 m and shallower (Amsler et al. 1995; Brouwer et al. 1995; DeLaca and Lipps 1976; Klöser et al. 1996; Valdivia et al. 2015) but we observed it deeper (even down to 35 m) at six sites, although not in abundance. Ko et al. (2020) also found *I. 'cordata'* deeper than 10 m at three of their six King George Island sites.

Sarcopeltis antarctica (previously *Gigartina skottsbergii*, Hughey et al. 2020) and *Trematocarpus antarcticus* were commonly observed across depths. *S. antarctica* was more commonly collected shallower and *T. antarcticus* was sometimes more common in middle depths, both of which are consistent with most northern WAP reports (Amsler et al. 1995; DeLaca and Lipps 1976; Klöser et al. 1996; Ko et al. 2020; Valdivia et al. 2015). The species presented in Figure 5 were primarily observed in middle to deeper depths, which, where reported, are also consistent with records from the northern WAP (Amsler et al. 1995; Brouwer et al. 1995; DeLaca and Lipps 1976; Klöser et al. 1996; Ko et al. 2020; Valdivia et al. 2015).

To our knowledge, the present study provides the only species-level information available on the vertical distribution of central WAP macroalgae. Moe and DeLaca (1976) and Mysterikou et al. (2014) provide species lists for 21 sites in the central WAP but no information on distribution by depth. Barnes and Brockington (2003) and Bowden (2005) provide limited data on macroalgal vertical distributions at Adelaide Island (Figure 1) but not by species. Although overall macroalgal cover is strongly, negatively correlated to annual sea ice cover (Amsler et al. 2023), which generally increases to the south (Figure 1), where present, most red macroalgal species' vertical distributions in the central WAP are similar to those previously reported in the northern WAP. However, few of the species were observed south of site J (66.1°S). The brown macroalgal flora of the central WAP differs markedly from that of the northern WAP due to the absence of *D. anceps* but the vertical distributions of the other two major overstory macroalgae, *D. menziesii* and *H. grandifolius* are similar to the northern WAP even though their percent cover becomes much lower.

Decreases in sea ice cover predicted by the end of the twenty-first century are likely to greatly increase overall macroalgal cover in the central WAP (Amsler et al. 2023), and glacier retreat, also driven by climate change, is likely to allow macroalgae to expand into newly exposed benthos (Deregibus et al. 2023). Both have important implications not only with respect to expanding benthic food webs but also to understanding the potential for the WAP to contribute to blue carbon sequestration (Amsler et al. 2023; Deregibus et al. 2023; Iken et al. 2023; Lagler et al. 2018; Morley et al. 2022). Our results indicate that with the likely exception of *D. anceps*, the distribution of macroalgae across depths in these expanded, future communities should be similar to

those in heretofore much more widely studied northern WAP communities. Consequently, current knowledge of the northern WAP should be applicable to predictions about food web structure and blue carbon sequestration in the future central WAP.

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