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Reviews and Syntheses: Carbon and Nitrogen Stable Isotope Analysis of Antarctic Macroalgae: a 35-Year Record for Environmental Change

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Abstract

Stable isotope analysis for Antarctic macroalgae has received minimal research interest outside of trophic ecology. However, carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analysis provides insights into nutrient uptake, productivity and response to environmental change. This review collates all available CN, $\delta^{15}N$ and $\delta^{13}C$ data available for macroalgae from the Antarctic continent. Fieldwork was also carried out in late 2023 to the northern West Antarctic Peninsula to collect specimens for stable isotope analysis. Prior to the 2023 survey, only 29 publications were found spanning a 35-year period from 1987−2022 with a strong bias towards data collection in the South Shetland Islands. A bias was found towards the Rhodophyta and Phaeophyta phyla, with *H. grandifolius* and *Desmarestia* sp. being the most studied species. This review highlights Antarctic seaweeds had a lower average CN compared to the global average, likely driven by the non-nitrogen limiting environment. Both $\delta^{15}N$ and $\delta^{13}C$ varied between species as well as spatially, $\delta^{13}C$ recorded a wider range (~25 ‰) than for $\delta^{15}N$ (~16 ‰). Spatial variation is assumed to be driven by site specific differences as well as latitudinal changes with light availability. $\delta^{13}C$ was more negative for the Rhodophyta phylum, with some species plotting below –30 ‰, however no significant difference was found between Rhodophyta and Phaeophyta species for $\delta^{13}C$ and all recorded average $\delta^{13}C$ values indicative of both passive CO_2 uptake and carbon concentration mechanism use. When plotted temporally, $\delta^{13}C$ showed variation with sea ice extent across the 35-year record. Within the last decade, both sea ice extent and macroalgae $\delta^{13}C$ became more variable and suggesting an unexplored link between primary producer response and sea ice instability. Significantly more research is required for stable isotope analysis of Antarctic seaweeds. Variability in both $\delta^{15}N$ and $\delta^{13}C$ will impact trophic food web studies, both spatially and temporally. There is a lack of data for sites outside of the Antarctic Peninsula as well as ~100 species currently having no data available. This review also highlights the potential for macroalgae to be an additional proxy for monitoring primary producer response to ongoing climatological changes for the Southern Ocean.

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1. Introduction

Macroalgae ecosystems are one of the most productive on Earth, covering an estimated 7.22 x10^6 km^2 (Duarte et al., 2022; Pessarrodona et al., 2019). Macroalgae are key primary producers after phytoplankton, with a net primary productivity (NPP) of 1.32 Pg C/year – noting that this is a conservative estimate with new habitats continually being documented (Duarte et al., 2022; Tait et al., 2024). Although Antarctic macroalgae contributes to less than 0.025% of the habitat area used in Duarte et al. (2022) to calculate NPP, these high latitude macroalgae environments are estimated to contribute up to 2.8% of global carbon fixation (Tait et al., 2024). Since new macroalgae environments continue to be discovered in the Southern Ocean the actual carbon fixation and role of macroalgae as a carbon sink may be much more (Robinson et al., 2022; Tait et al., 2024). There are 151 Antarctic macroalgae species currently identified, although new species are being discovered as new field locations are explored (Oliveira et al., 2020; Pellizzari et al., 2023). Over 40 % of these species are endemic (Oliveira et al., 2020), which stems from the formation of the Antarctic Circumpolar Current (ACC) ~30-million-years ago, isolating the continent from the rest of the world's oceans, effectively becoming barrier to species migration (Oliveira et al., 2020; Sanches et al., 2016). Modern Antarctic macroalgae are well-adapted to the extreme cold, nutrient regime and prolonged low-light periods due to this long evolutionary timeline of isolation by the ACC and limited environmental change (Convey and Peck, 2019; Wiencke and Amsler, 2012).

Macroalgae biomass, distribution and abundance will vary according to environmental conditions more favourable for growth. Parameters include, but are not limited to, temperature, sea ice and light availability for photosynthesis (Clark et al., 2017). Strong seasonal light trends mean the lower Antarctic latitudes receive more daylight hours in the winter/autumn period, and importantly more photosynthetically available radiation (PAR) for primary producers (Schwarz et al., 2003). An inverse relationship exists between macroalgae abundance, cover and species richness with latitude, resulting in biodiversity "hotspots" such as the South Shetland Islands (SSI) (Fig. 1) (Pellizzari et al., 2023; Sanches et al., 2016; Wiencke et al., 2007). Macroalgae cover can drop from > 80 % in the SSI to < 7 % at high Antarctic latitudes such as at Adelaide Island in the south of the Peninsula (Fig. 1) (Amsler et al., 1995, 2023; Iken et al., 2023; Wiencke and Amsler, 2012). Sea ice further regulates this biological pump for the Southern Ocean; irradiance and PAR are intrinsically linked to sea ice extent, thickness and duration (Lohrer et al., 2013; Massom and Stammerjohn, 2010). Thicker sea ice significantly decreases PAR; reduced macroalgae cover has been widely associated with increased sea ice across both the West Antarctic Peninsula (WAP) and Ross Sea due to reduced PAR (Clark et al., 2017; Iken et al., 2023; Lohrer et al., 2013).

The WAP region has been studied for many decades one of these biodiversity hotspots, and climate modelling indicates that this region is particularly vulnerable to climate change impact. The WAP is one of the fastest warming regions on Earth (0.46 ± 0.15 °C per decade) (Bromwich et al., 2013; Clark et al., 2017; Ducklow et al., 2012; Pellizzari et al., 2023). Marine heatwaves are increasingly common and severe in the northern WAP, with 12 recorded between 2022 and 2023 alone, six of which were labelled as "strong" and one "extreme" (Pellizzari et al., 2025). Seawater temperatures of 4–8 °C can halt gametophyte reproduction in some *Desmarestiales*;

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prolonged marine heatwaves therefore have the potential to halt reproduction and even cause irreversible morphological damage to sporophytes (Matula et al., 2022; Pellizzari et al., 2025). Temperature rise may favour certain species such as *P. decipiens*, for example, or allow for invasive species such as *Durvillaea antarctica* to establish (Marcías et al., 2017; Pellizzari et al., 2017).

Although sea ice dynamics are considered the dominant control over macroalgae distribution, productivity and assemblage the impact of retreating glaciers cannot be ignored, especially for lower latitude Antarctic coastlines (Clark et al., 2017; Lohrer et al., 2013). High sedimentation and turbidity negatively impact PAR. In the northern WAP meltwater can have a closer association with irradiance than sea ice; the increased sedimentation rate can reduce PAR to below the photon fluorescence required for certain macroalgae species (Deregibus et al., 2025). Annual daily irradiance at the Fourcade Glacier in Potter Cove (SSI) is > 300 % lower in areas with high glacier influence compared to areas with low glacier influence and does not meet the minimum requirements of species such as *H. grandifolius* and *P. decipiens* (Deregibus et al., 2025). This can significantly reduce the ability of primary producers, including macroalgae, to photosynthesise, grow and reproduce. However, much more research is required to understand, monitor and predict current and future communities' response and changes to ongoing climate change across the WAP region (Pellizzari et al., 2025).

Modern ecosystem dynamics and their response to climate and environmental change can be traced through carbon and nitrogen stable isotope analysis (Hobson, 2023; Pethybridge et al., 2018; Sánchez-Carrillo and Álvarez-Cobelas, 2018) and the Redfield ratio (Ratnarajah et al., 2023; Tanioka et al., 2022). Stable isotope analysis of macroalgae has been a topic of research for over five decades, commonly used in Europe, North America and Australia (García-Seoane et al., 2018; Raven et al., 1995; Samper-Villarreal, 2020). Trophic ecology utilises both carbon ($\delta^{13}C$) and nitrogen isotopes ($\delta^{15}N$) to trace energy transfer and trophic structure within an ecosystem (Dunton, 2001; Gillies et al., 2012a; Hobson and Welch, 1992). Publications by Atkinson and Smith (1983) on marine macrophyte Redfield Ratios and research from Stephenson et al. (1984), Maberly et al. (1992) and Raven et al. (1995) on stable isotopes were influential in our understanding of macroalgae ecophysiology, photosynthesis and nutrient uptake. To enhance the visibility and future directions for macroalgae research in polar regions, this review has been conducted to compile all available biogeochemical macroalgae data for the Antarctic and sub-Antarctic region. No such review of this data has been conducted and as such our understanding of spatial and species biases is poor. This review will identify both spatial and species gaps in the available literature, as well as assess biogeochemical trends relating to spatial, environmental and phylogenetic controls. We will also contribute our own biogeochemical data from eight new field sites across the northern WAP region.

1.1 History of biogeochemical research for Antarctic macroalgae:

Antarctic macroalgae biogeochemistry is a relatively recent field of study; the first data was generated less than 50 years ago (Fischer and Wiencke, 1992) (Fig. 2). Prior to 1987, work primarily focused on taxonomy, distribution and life cycles of species such as *H. grandifolius*

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and the *Desmarestiales* (Dieckmann et al., 1985; Hastings, 1977; Moe and Silva, 1977). Almost a decade later, Dunton (2001) was the first to publish $\delta^{13}C$, $\delta^{15}N$ and CN in a single study for Antarctic seaweeds. Figure 2 shows sporadic publications over the next 15 years or so; studies are especially limited in their number of individual analyses and often do not include CN data. In the ~20 years since Dunton (2001) publications have focussed on the wider Antarctic food web (Caputi et al., 2020; Choy et al., 2011; Gillies et al., 2012a; Norkko et al., 2007). Macroalgae was collected sporadically or with the focus shifting to higher up the food chain. The next significant survey of macroalgae wasn't until Cardona et al. (2021) published their results linking isotopic variation in the benthic food web with latitude. Iken et al. (2023) expanded on this with a 2019 survey of 15 sites across the WAP. These two publications represent over half of the available biogeochemical data for the Antarctic continent. But the data is overwhelmingly skewed towards the WAP (Fig. 1). Over half of the publications in Figure 2 are from the WAP, representing more than 80% of individual analyses. The peninsula's long-held status as the fastest warming environment on earth has generated significant scientific and media interest (Olischläger et al., 2014; Pellizzari et al., 2023). King George Island (Fig. 1) has been repeatedly surveyed along its southern coastline over the last three decades (Ahn et al., 2021; Alkemade and Van Rijswijk, 1993; Choy et al., 2011; Corbisier et al., 2004; Fernández et al., 2024; Fischer and Wiencke, 1992; Ha et al., 2019; Iñiguez et al., 2019; Pasotti et al., 2015; Rosenfelder and Vetter, 2012; Weykam et al., 1996; Zenteno et al., 2019). Biogeochemical data is therefore disproportionately represented by the SSI, an area of less than 500 square miles and north of the Antarctic circle. Slower progress has been made in collecting biogeochemical data from elsewhere and means East Antarctica is represented by only 8 studies from the bases of McMurdo, Dumont d'Urville, Davis and Casey (Fig. 1) (Caputi et al., 2020; Gillies et al., 2012a, b, 2013; Michel et al., 2019; Norkko et al., 2004, 2007; Runcie and Riddle, 2006). Only Gillies et al. (2013) has repeatedly collected macroalgae in East Antarctica, surveying the Windmill Islands in the early 2000s (Gillies et al., 2012a, b) and then the Vestfold Hills between 2009–10 (Gillies et al., 2013).

Large scale surveys are beneficial for the wider scientific community. Already Iken et al. (2023) has 19 citations, widely used in assessing trophic ecology (Oswalt et al., 2025; Whippo et al., 2024) and sources of sediment organic matter for the WAP (Bisch et al., 2024). Large surveys contribute a significant amount of data to the literature, but continued repetition is required to assess baseline shifts and changes (Cardona et al., 2021; Gillies et al., 2012a). This will become increasingly important as Antarctica experiences accelerating biological and climatological change (Convey and Peck, 2019; Ducklow et al., 2012; Norkko et al., 2007). As Figure 2 shows with Dunton (2001), it should not take another ~20 years for a similar biogeochemical survey of Antarctic macroalgae after Iken et al. (2023).

1.2 Stable Isotope Analysis of Macroalgae

Carbon Isotopes: On their own, $\delta^{13}C$ analyses are utilised as a method of identifying whether a species takes up carbon as CO_2 via passive diffusion or actively uptakes HCO_3^- (a method requiring a Carbon Concentration Mechanism, or CCM) (Maberly et al., 1992; Raven et al.,

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1995). Isotopic values between 0 ‰ to –10 ‰ suggest HCO_3^- uptake, whilst values < –30 ‰ indicate solely passive uptake of CO_2 (Fig. 3). Macroalgae with $\delta^{13}C$ values between –30 ‰ and –10 ‰ are generally thought to be using both CO_2 and HCO_3^-, changing the CCM based on changing environmental conditions (Fig. 3). Macroalgal $\delta^{13}C$ shows strong species-specific variation; > 60% of Antarctic Rhodophyta phylum, for example, lack a CCM and therefore record lower $\delta^{13}C$ values (Fernández et al., 2024; Maberly et al., 1992; Raven et al., 1995; Raven and Hurd, 2012). Fernández et al. (2024) found 16 species of Rhodophyta displaying values below –30 ‰; the Rhodophyta *Paraglossum salicifolium* averaged < –38.2 ‰ ± 0.4 ‰, the lowest of all species analysed. Carbon isotope ratios as a function of depth have received less attention, but shallow, inter-tidal environments with high irradiance have been associated with higher $\delta^{13}C$ values in both field (Fernández et al., 2024; Iken et al., 2023) and laboratory (Wiencke and Fischer, 1990) conditions. Conversely, sub-tidal macroalgae tend to record lower $\delta^{13}C$ values where photosynthetic rates are reduced due to low irradiance (Dyer et al., 2019; Fischer and Wiencke, 1992; Gómez and Huovinen, 2015). Reduced carbon requirements in light-limited environments indicate that carbon demands may be met by passive uptake of CO_2 as opposed to employing a CCM. This would drive the $\delta^{13}C$ towards more negative values (Maberly et al., 1992; Raven et al., 2002). Therefore, carbon isotopes in macroalgae can be used to infer environmental conditions and photosynthetic processes.

Nitrogen Isotopes: The Southern Ocean is characterised by high nitrate concentrations; rarely is nitrogen the limiting factor in marine productivity (Brault et al., 2018; DiFiore et al., 2009; Dittrich et al., 2022; Henley et al., 2017). However, localised effects on $\delta^{15}N$ will arise from differing environmental conditions and can be used to understand local ecosystem dynamics that will imprint in trophic web analysis. Since macroalgae reflect the $\delta^{15}N$ signature of the environment in which they are growing with minimal fractionation, this makes them excellent environmental proxies (Peterson and Fry, 1987; Viana and Bode, 2013). Nitrogen isotopes ($\delta^{15}N$) have dominantly been used to discriminate between different nutrient sources. Seabird guano, for example, is ^{15}N-enriched in comparison to the "natural" oceanic nitrate signature of +4.8 ‰, typical of the deep ocean (Sigman et al., 2000), while other studies suggest oceanic values between +3 ‰ and +4 ‰ (DiFiore et al., 2009; Wainright et al., 1998; Sigman et al., 2000; Wang et al., 2020). Guano may be elevated in $\delta^{15}N$ > +30 ‰ (Lucassen et al., 2017) and as such is an easily identifiable signature compared to surface water $\delta^{15}N_{NO3}$ (~ +6.5 ‰) and coastal waters (~ +8 ‰) which can overlap with pack ice surface water values between +3.2 – +9.0 ‰ recorded in some studies (Cozzi and Cantoni, 2011; Dittrich et al., 2022; Henley et al., 2020). The Southern Ocean $\delta^{15}N$ signature has seasonal variability, influenced by the timing of phytoplankton blooms in the euphotic zone (Brault et al., 2018; Henley et al., 2017; Sigman and Fripiat, 2019). Spring ice retreat, rising temperatures and light availability triggers phytoplankton productivity resulting in blooms (Henley et al., 2017). Phytoplankton preferentially uptake isotopically light nitrate (NO_3^-) leaving the residual nitrogen pool ^{15}N-enriched (Brault et al., 2018; Henley et al., 2017). Elevated $\delta^{15}N$ signatures have been recorded for Ryder Bay, Adelaide Island during the peak phytoplankton bloom, especially towards the end of the growing season, to values > +10 ‰ (Henley et al., 2017).

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Localised variation in nutrient concentrations, iron concentration, meltwater influence and sea-ice dynamics will cause differences in timing, duration and size of phytoplankton blooms (Dittrich et al., 2024; Brault et al., 2018; Joy-Warren et al., 2019). Nitrogen recycling (i.e., nitrification) produces nitrate with a lower $\delta^{15}N$ signature, a phenomenon more pronounced under lower light conditions in the surface ocean when nitrogen concentrations are reduced (Fripiat et al., 2015; Henley et al., 2017). Nutrient concentrations may influence nitrification rates during a phytoplankton bloom, thus lowering the $\delta^{15}N$ signature locally (Fripiat et al., 2015). Higher ammonia concentrations paired with lower $\delta^{15}N$ values would suggest a high degree of nitrification (Henley et al., 2017). Henley et al. (2017) recorded a ~ 4 ‰ decline from the upper 15 metres down to 500 metres for Adelaide Island (Fig. 1) pointing towards a depth control over $\delta^{15}N$ too.

CN Ratio: Carbon and nitrogen content (wt% C, wt% N) of macroalgae has been employed as a measure of nutritional quality, nutrient limitation and carbon storage (Sheppard et al., 2023; Wiencke et al., 2007). Nutrient limiting environments are identified through calculation of the Redfield Ratio: the ratio of carbon to nitrogen to phosphorus (Redfield, 1934). Atkinson and Smith (1983) adapted this for macroalgae, reporting a CN ratio of 18.4 suggesting macroalgae have greater capacity for carbon uptake and storage than phytoplankton. A more recent assessment by Sheppard et al. (2023) indicates a macroalgae CN of 20.2. Geographical variation of CN ratios is linked to varying upwelling regimes causing high nutrient environments (Atkinson and Smith, 1983; Peters et al., 2005; Raven et al., 2002; Wessels et al., 2006). Southern Ocean macroalgae generally have higher CN ratios than their Arctic counterparts, for example, since the Southern Ocean is not nitrogen limited. The macroalgae thallus can also influence CN ratios; more complex and larger structures require a higher carbon demand (Dyer et al., 2019; Henley and Dunton, 1995). The age of photosynthesising tissue has also been documented as influencing CN; higher growth rates associated with younger tissue can accelerate carbon demands and therefore increase the CN ratio (Sato et al., 2025; Sjøtun et al., 1996; Weykam et al., 1996). Multiple factors influence CN; reflecting changes in environment, nutrient limitation, photosynthesis and productivity (Korb and Gerard, 2000; Sato et al., 2025; Weykam et al., 1996). They are an important tool in understanding the wider biogeochemical dataset and are an important mechanism to use alongside isotopic data.

2. Methodology:

Between November and December 2023 macroalgae was collected from eight sites across the northern WAP and SSI (Fig. 1). Fieldwork was undertaken in collaboration with the expedition cruise operator Viking from onboard Viking Polaris. All field sites are classified as International Association of Antarctic Tour Operators (IAATO) designated landing sites. The Antarctic tourist industry has grown exponentially over the past two decades, supporting small research projects around the WAP. The fieldwork was focussed around two main objectives: (1) to collect and produce a large sample set of *H. grandifolius* for incremental isotope analysis; and (2) to collect inter-tidal macroalgae from across the guest landing sites. Sub-tidal macroalgae was sampled using the Blueye underwater remote operated vehicle (ROV) from onboard a

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zodiac. Specimens were collected between a water depth ranging from 5 to 50 metres over a series of 2-hour dive intervals. Inter-tidal macroalgae were collected by hand during the tourist landing operations. Specimens were frozen immediately and then dried on return to the Stable Isotope Biogeochemistry Laboratory at Durham University.

Dried specimens were sub-sampled and weighed between 1.5 and 2.0 mg into tin capsules for stable isotope analysis. Carbon isotopes are reported against Vienna Pee Dee Belemnite (VPDB) and nitrogen isotopes are reported against atmospheric nitrogen (AIR). Accuracy is monitored with international standards (e.g., IAEA-600, IAEA-N2 and USGS 44) and against in-house standards (e.g., spirulina, urea and a-cellulose). Analytical uncertainty is ± 0.1 (1sd) for replicate analyses.

2.1 Database Generation:

This review includes publications that produced $\delta^{13}C$, $\delta^{15}N$, wt% carbon and wt% nitrogen data from Antarctic macroalgae. Keywords “Macroalgae” “Stable Isotopes”, “Carbon”, “Nitrogen” and “Antarctica” were inputted into Google Scholar. This returned 4,860 results that were filtered for their relevance for biogeochemical analysis of Antarctic seaweeds. Studies were only considered if they had generated their own analyses to avoid repetition of the data. In total, 29 papers were found that had generated their own biogeochemical data from the Antarctic and Sub-Antarctic region. The tool Research Rabbit was used to check for linked or relevant studies that were potentially missed through the initial Google™ Scholar search. In one instance the corresponding author (Cardona et al., 2021) was contacted to provide their data that was not initially available through a data repository.

The carbon and nitrogen biogeochemical data was compiled (see Supplementary data file). No correction for the Suess Effect has been made and all $\delta^{13}C$ values are the same as that reported in their respective publications. The relatively short period (~40 years) means the global decrease in marine $\delta^{13}C$ values from the Suess Effect would be insignificant in the context of this review (Dombrosky, 2020; Eide et al., 2017). Additional metrics were included such as location, species, date and water depth, although this was not always possible. Laboratory experiments utilising macroalgae collected from Antarctica have been included but the data has not been analysed in combination with field data. Excel and R Studio 4.4.1 (R Core Team) were used to process and analyse the database results with figures produced using ArcGIS and Adobe Illustrator.

3. Results & Discussion:

3.1 This study:

This study collected 99 inter-tidal macroalgae specimens from eight field sites (Fig. 1): 7 *A. utricularis*, 4 *Desmarestia* sp., 10 *I. cordata*, 35 *Monostroma* sp. and 43 *P. decipiens*. A further 9 *H. grandifolius* were collected from four sites between 5 and 50 metres depth. The *H. grandifolius* blades were incrementally sub-sampled and produced a total of 589 $\delta^{13}C$, $\delta^{15}N$

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and CN analyses. In total, this study produced 688 biogeochemical analyses, or 2064 data points, making this the largest biogeochemical study of Antarctic macroalgae to date that we are aware of (Fig. 2). The data generated from this survey provides more biogeochemical data than the 29 papers included in our literature analysis combined.

The 2023 data recorded a smaller range (16.2) between 4.4 (*P. decipiens*) and 20.7 (*H. grandifolius*) for CN compared to the database (Figs. 4A and 5A). Chlorophyta CN averaged 7.4 ± 1.3 (*n=35*), slightly lower than Rhodophyta at 7.3 ± 2.0 (*n=52*). The Phaeophyta phylum was significantly higher at 16.4 ± 1.7 (*n=600*). A one-way ANOVA indicated a significant difference in CN was found between species ($F_{5,681}$ = 654.8, $p < 0.001$). A Tukey post-hoc comparison test confirmed *H. grandifolius* was significantly higher than all other species ($p < 0.001$). *H. grandifolius* recorded the highest average (16.6 ± 1.4, *n=589*) compared to all other species whilst *P. decipiens* was the lowest (6.9 ± 2.0, *n=43*) (Fig. 5A). The 2023 $\delta^{15}N$ recorded a range of (15.8 ‰), between –1.1 ‰ (*H. grandifolius*) and +14.7 ‰ (*Monostroma* sp.). $\delta^{15}N$ was highest for the Chlorophyta phylum (+7.7 ± 4.1 ‰, *n=35*) (Fig. 5B). The Rhodophyta phylum averaged +4.5 ± 0.7 ‰ (*n=52*) and Phaeophyta produced the lowest $\delta^{15}N$ average (+1.9 ± 1.0 ‰, *n=600*). After a one-way ANOVA confirming species had significantly different $\delta^{15}N$ values ($F_{5,681}$ = 163.5, $p < 0.001$), a Tukey post-hoc comparison test found *Monostroma* sp. to be significantly higher than all other species ($p < 0.001$) whilst *H. grandifolius* was significantly lower ($p < 0.001$). *Monostroma* sp. averaged +7.7 ± 4.0 ‰ (*n=35*) and *H. grandifolius* had the lowest $\delta^{15}N$ average at+1.8 ± 1.0 ‰ (*n=589*) (Fig. 5B). For $\delta^{13}C$ the 2023 data is comparable to the database range of 24.9 ‰ (Fig. 4C). $\delta^{13}C$ values ranged between –34.7 ‰ (*H. grandifolius*) and –9.8 ‰ (*Iridaea* sp.) for this study (Fig. 5C). Rhodophyta was the most elevated phylum (–16.4 ± 3.1 ‰, *n=52*), and plots > 5 ‰ higher than the Chlorophyta (–21.7 ± 2.5 ‰, *n=35*) and Phaeophyta (–23.2 ± 4.7 ‰, *n=600*) phyla. A one-way ANOVA confirmed species were significantly different in $\delta^{13}C$ ($F_{5,681}$ = 32.5, $p < 0.001$) and a Tukey post-hoc comparison test confirmed *A. utriculares* was significantly enriched in ^{13}C compared to *Desmarestia* sp. ($p = 0.016$), *H. grandifolius* ($p < 0.001$) and *Monostroma* sp. ($p = 0.001$). *P. decipiens* was also significantly enriched compared to *Monostroma* sp. and *H. grandifolius* ($p < 0.001$). No significant differences were observed between remaining species. *A. utriculares* recorded the least negative $\delta^{13}C$ average value of –12.9 ± 2.1 ‰ (*n=7*); *H. grandifolius* was the most negative (–23.4 ± 4.6 ‰, *n=589*) (Fig. 5C).

3.2 Database Summary:

Macroalgae biogeochemical data was collated from studies between 1987 and 2022 from 29 publications. Three studies are laboratory experiments (Iñiguez et al., 2019; Sáez et al., 2023; Wiencke and Fischer, 1990); this data has been included in the database but is omitted from figures comparing field data. A recent publication by Frontier et al. 2026) used isotopically enriched macroalgae and has not been included in this review, but it represents one of the few experimental studies for Antarctica. A regional bias was found with half of the macroalgae data from the WAP, representing 77% of the biogeochemical data (Fig. 1). Of these 15 studies, 13 were based in the SSI (Fig. 1). In total, 598 × $\delta^{13}C$, 498 × $\delta^{15}N$ and 536 × CN analyses have

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been published over a 35-year period (Fig. 2) and 60 different species have been investigated: 37 Rhodophyta, 13 Phaeophyta and 10 Chlorophyta. As a single species *H. grandifolius* has the most data entries (73), but *Desmarestia* sp. has the most published results for one genus. A total of 87 entries were found for *D. anceps*, 57 for *D. menziesii* and 33 for *D. antarctica*.

These large brown seaweeds dominate the sub-tidal biomass and are easily identifiable (Amsler et al 1995; Wiencke; Fischer & Wiencke). Identification of the smaller, more delicate species such as *Lambia antarctica* or *Porphyra endiviifolium*, for example, is much harder. Almost all studies employed SCUBA as a method of collection, favouring larger species such as the *Desmarestiales* that thrive > 10 m depth that have >100 analyses. The wide depth range of ~5 m to an estimated 90 m depth; the likelihood of finding and collecting these large browns, or depth tolerant reds such as *P. decipiens*, is greater than species restricted to the upper littoral zone (Wiencke et al., 2007). *Desmarestiales* are key primary producers, along with *H. grandifolius* (> 70 data entries), that underpin much of the Antarctic food web making them popular with trophic ecologists. The less well studied Chlorophyta are restricted to the upper sub-tidal or shallow rockpools meaning they are omitted from many SCUBA surveys. In total there are only 19 Chlorophyta $\delta^{15}N$ data points (Fig. 4B), a single species of Phaeophyta has three times this number. Further issues arose with poor identification of species. Caputi et al. (2020) for example contains data for "Epiphytes" without any further identification. Others listed algae as "Sympagic Red" or simply "Unidentified Algae" (Alkemade and Van Rijswijk, 1993; Michel et al., 2019); this does not benefit the wider literature as biogeochemical interactions are often species specific. As much information as possible is required to fully understand the dataset.

3.3 CN Overview:

The database CN has a range between 5.6 (*Urospora penicilliformis*) and 18.2 (*Lambia antarctica*) for Chlorophyta, 3.8 (*Chordaria linearis*) and 24.8 (*H. grandifolius*) for Phaeophyta and 4.1 (*Myriogramme smithii*) and 23.8 (*Crystoclorium obtusangulum*) in Rhodophyta. Upon inclusion of Coraline algae the CN range extends to 50.7 (Azcárate-García et al., 2025). These have been removed from Figure 4A as significant outliers. No significant difference is evident between database CN values for Chlorophyta and Rhodophyta, with phyla averaging 8.8 ± 2.2 (*n=41*) and 8.7 ± 2.6 (*n=284*), respectively (Fig. 4A). Including the Coraline algae outliers the Rhodophyta CN average increases to 9.3 ± 5.2 (*n=290*), still showing no significant difference. CN values were significantly different for Phaeophyta, with an average of 13.9 ± 3.9 (*n=206*) (Fig. 4A). A Levene's test indicated that CN variance differed significanty between phyla ($F_{2,527}$ = 15.67, $p < 0.001$). A Kruskal-Wallis test was used and found a significant difference between phyla ($\chi^2_2 = 223.3$, $p < 0.001$). A Dunn's post-hoc test with Bonferroni correction confirmed no significant difference exists between Chlorophyta and Rhodophyta (p = 1.00). But Phaeophyta showed a significantly higher CN than both Chlorophyta and Rhodophyta (both $p < 0.001$). CN data from this study aligns with the database trend in that Phaeophyta plots significantly higher than Chlorophyta and Phaeophyta (Fig. 4A). No significant difference is evident between our study and the database values, although our Phaeophyta data does plot higher than the database

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Phaeophyta. This study's Phaeophyta data is skewed towards *H. grandifolius*, therefore this species bias could be driving the discrepancy between our study and the wider database for this phylum (Figs. 4–6).

The phylogenetic difference in CN, where the Phaeophyta phyla is higher by ~ 6 (Fig. 4A), was identified in macroalgae across the Antarctic continent regardless of study, site or depth. Higher CN vales for Phaeophyta is a global phenomenon, also replicated in our 2023 survey (Figs. 5 and 6) (Atkinson and Smith, 1983; Sheppard et al., 2023). However, Antarctic macroalgae consistently record average lower CN values when compared to the global averages of 18.4 and 20.2 defined by Atkinson and Smith (1983) and Sheppard et al. (2023), respectively (Fig. 6). Instead, the Antarctic dataset is more closely aligned with the lower CN average defined by Duarte (1992) at 16.3. All three phyla have lower CN averages than their global counterparts. Chlorophyta and Rhodophyta plot ~10 less than their phyla's global average; for Antarctic Phaeophyta this difference is almost 14 (Fig. 6) (Sheppard et al., 2023). None of the Antarctic phyla average > 20, the threshold for a nitrogen limited environment (Hurd et al., 2014). This offset suggests Antarctic macroalgae contain comparatively more nitrogen (Fig. 6) (Wiencke and Amsler, 2012). The Southern Ocean is associated with year-round high DIN concentrations (Henley et al., 2020); it is unsurprising that the Antarctic macroalgae are recording higher nitrogen contents than their temperate and tropical counterparts (Sheppard et al., 2023). As with the global macroalgae CN ratio, the Antarctic CN ratio is greater than the Redfield Ratio of 6.6 (Redfield, 1934).

Phylogenetic differences are in line with the same global trend of low CN in Phaeophyta (Sheppard et al., 2023). Only one example of *Desmarestia antarctica* recorded anomalously high Nitrogen, collected by Iken et al. (2023). Photosynthetic pigments differ between the three phyla. For example, chlorophylls and phycobiliproteins are nitrogen rich compounds present in Chlorophyta and Rhodophyta, respectively (Harrison and Hurd, 2001; Hurd et al., 2014). Presence, or lack of, these nitrogen rich compounds will therefore drive the %Nitrogen variation between species. The lower nitrogen content for Phaeophyta may also stem from an inability to effectively store nitrogen (Korb and Gerard, 2000). The kelp like Antarctic species *H. grandifolius* was found to lack storage capacity for nitrogen when compared to N. Atlantic *Laminariales* (Korb and Gerard, 2000). This trend was not studied for Chlorophyta or Rhodophyta. So, whilst the Antarctic Phaeophyta do seem to contain less nitrogen, they still record a higher nitrogen content than their temperate and tropical counterparts so their storage capacity must be greater, or they are incorporating less carbon (Atkinson and Smith, 1983; Sheppard et al., 2023).

Low CN ratios are theorised to be a result of protein content in the more delicate foliose/feathery species (i.e., Chlorophyta and/or Rhodophyta) (Weykam et al., 1996). Antarctic diatoms display "antifreeze" like enzymes (i.e., nitrogen containing protein); the observed lower CN ratio may be linked to the presence of cold adapted enzymes and/or amino acids in the Antarctic seaweeds (Dieckmann et al., 1985; Gómez et al., 2009). Antarctic macroalgae are exceptional cold-adapted species: endemic species are capable of metabolic processes down to 0 ˚C (Gómez et al., 2009; Wiencke and Amsler, 2012). The significantly higher nitrogen content for Rhodophyta may also reflect this specialisation; many more

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Rhodophyta are endemic to Antarctica and capable of growth in the highest latitudes, therefore likely possessing suitably adapted compounds to cope with extreme low temperatures (Gómez et al., 2009; Oliveira et al., 2020; Raven et al., 2002). Therefore, the phylogenetic variation in CN for the Antarctic macroalgae may go beyond simply pigment variation between the red, green and brown seaweeds. Peters et al. (2005) did not find a correlation between the CN ratio and protein content for several Antarctic species. However, our review includes almost twice the number of species analysed in Peters et al. (2005) that shows a clear offset between Antarctica and the global average (Fig. 6) that can be explained by the high DIN environment, but we would argue more work is required to assess whether this is also a biological response to extreme low temperatures.

Desmarestia sp. and *H. grandifolius* drive the high CN value for the Phaeophyta phylum; they represent 84% of the Phaeophyta dataset and average >30 for carbon content. By contrast, nitrogen content is only ~2. Although both species are endemic to Antarctica, they display similarities to the *Laminariales* (i.e., kelp) of the N. Atlantic and Arctic as large brown seaweeds (Bolton, 2010; Raven et al., 2002; Surif and Raven, 1990). Large seaweeds are characterised by high carbon demands, increased frond size requires more carbon to maintain structure, size and maintain a fast growth rate; thus, increasing the CN ratio (Hurd et al., 2014; Sheppard et al., 2023). Smaller Phaeophyta (e.g., *A. utriculares*) have lower CN values and plot more similarly to the inter-tidal Rhodophyta and Chlorophyta (Fig. 5A). The lower growth rate and smaller, more delicate structure compared to the larger Phaeophyta results in a reduced carbon demand; ultimately reducing the CN ratio and potential for carbon storage (Harrison and Hurd, 2001; Hepburn et al., 2011; Sheppard et al., 2023). Variation in CN will also result from differing tissue compositions; especially in the larger macroalgae (Dyer et al., 2019). Internal CN variation is likely driven by differing carbon demands between meristematic tissue compared to older blade tips. Photosynthesis, respiration and growth are basal in *H. grandifolius* (Drew and Hastings, 1992); the meristem will therefore have a greater carbon, and nitrogen, demand compared to the apical tip of the blade (Dyer et al., 2019; Zhou et al., 2015). Seasonal light and temperature influence on carbon and nitrogen content is inconclusive for Antarctic macroalgae. Macroalgae tissue is likely to reflect either high, or low, growth rates depending on the time of sampling.

Since only 60 of the >150 Antarctic macroalgae have CN information it is likely the Antarctic CN average could change in future as more species are added. Our 2023 Rhodophyta data suggest a greater N content compared to the wider database (Fig. 6B), whilst Phaeophyta and Chlorophyta are relatively similar to the database (Fig. 6B). The offset between Antarctica and the global average may be more apparent due to the high degree of endemism in Antarctica (Oliveira et al., 2020). Many species included do not grow outside of the Southern Ocean and as such they are highly specialised to the cold, high DIN environment (Gómez and Huovinen, 2015; Henley et al., 2020; Raven et al., 2002). So, whilst high DIN and high N assimilation is likely to be the controlling factor on the CN, some deviation may stem from the incomplete sample set that contains species unique to that environment. Significantly more information is required to more accurately assess the nutritional quality of Antarctic macroalgae and carbon storage potential. Estimates of carbon storage will be mainly influenced by the Phaeophyta

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(i.e., *H. grandifolius* and *Desmarestia* sp.) but prior to our survey there were fewer than 100 analyses for the entire continent. With a predicted poleward expansion of macroalgae forests, the carbon sequestration potential in Antarctic seaweed is likely to increase. But more data is needed to accurately quantify, monitor and predict changes of this blue carbon store.

3.4 Stable Isotopes:

The database displays comparable trends in both $\delta^{15}N$ and $\delta^{13}C$ with our results for the 2023 survey (Figs. 4 and 5). In both our data and the database all three phyla have a significantly smaller $\delta^{15}N$ range compared to $\delta^{13}C$ (Figs. 4 and 5). For the database, Chlorophyta records the highest range from +0.8 ‰ (*L. antarctica*, Fildes Bay) to +13.8 ‰ (Snow Algae, Anvers Island), note that snow algae may be terrestrial, or on the sea ice. The macroalgae *Monostroma hariotii* records the second highest $\delta^{15}N$ value for Chlorophyta at +9.4 ‰, also from Anvers Island (Dunton, 2001). This is < 5 ‰ lower than our 2023 survey's highest *Monostroma* sp. value at +14.7 ‰. Rhodophyta had a $\delta^{15}N$ range of 10.8 ‰ for the database, *Phyllophora antarctica* recording the highest (+8.8 ‰) and lowest (–2 ‰) values. Database $\delta^{15}N$ values for Phaeophyta record a smaller range compared to the other phyla (–1 ‰ to +9.7 ‰, *H. grandifolius* from the WAP and Dumont d'Urville, respectively). The 2023 survey is only slightly depleted in comparison to the wider database Phaeophyta values (Fig. 5B). Database Chlorophyta has a slightly higher $\delta^{15}N$ average value (+5.2 ± 2.8 ‰, *n=19*) than Rhodophyta (+3.4 ± 1.6 ‰, *n=301*) and Phaeophyta (+2.8 ± 1.6 ‰, *n=178*) database values (Fig. 5B). A Levene's test indicated that $\delta^{15}N$ variance differed significantly between phyla ($F_{2,495} = 4.01$, $p < 0.019$). A Kruskal-Wallis test found a significant difference between phyla ($\chi^2_2 = 28.54$, $p < 0.001$). A Dunn's post-hoc test with Bonferroni correction confirmed all phyla were significantly different in $\delta^{15}N$. Chlorophyta was more positive than both Phaeophyta ($p < 0.001$) and Rhodophyta ($p < 0.011$). Rhodophyta was also significantly more enriched in ^{15}N than the Phaeophyta phylum ($p < 0.001$).

The $\delta^{13}C$ database has a range of 25 ‰ for Chlorophyta, 29.4 ‰ for Phaeophyta and 32.5 ‰ for Rhodophyta (Figure. 4C). The least negative $\delta^{13}C$ value was –8.3 ‰ from *Adenocystis utricularis* (Phaeophyta) whilst the lowest, –38.2 ‰, was from *Paraglossum salicifolium* (Rhodophyta). Both are from the SSI (Fig. 1). A laboratory experiment produced the lowest $\delta^{13}C$ Phaeophyta result from *H. grandifolius* (–37.6 ‰) (Wiencke and Fischer, 1990). The lowest field value was –35.9 ‰ for *Halopteris obovata* from Fildes Bay (Fernández et al., 2024). A Coralline species had the highest Rhodophyta $\delta^{13}C$ value at –5.8 ‰ (Cardona et al., 2021). Chlorophyta ranged between –10.2 ‰ (*Ulva intestinalis*, Cape Evans) and –35.2 ‰ (*Lambia antarctica*, Fildes Bay). Chlorophyta produced the highest average $\delta^{13}C$ value: –19.7 ± 5.8 ‰, *n=41*. Followed by Phaeophyta (–24.4 ± 5.6 ‰, *n=230*) and then Rhodophyta (–25.7 ± 8.3 ‰, *n=327*). Figure 4C shows bunching of Rhodophyta datapoints from ~ –25 ‰ to ~ –15 ‰ and then at ~ –35 ‰ and has likely caused the higher standard deviation. A Levene's test found unequal variance between phyla for $\delta^{13}C$ ($F_{2,595} = 49.00$, $p < 0.001$) and subsequent Kruskal-Wallis test confirmed $\delta^{13}C$ was significantly different between phyla ($\chi^2_2 = 26.66$, $p < 0.001$). A Dunn's post-hoc test with Bonferroni correction indicated Chlorophyta has

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significantly more positive $\delta^{13}C$ values compared to both Rhodophyta and Phaeophyta (both $p < 0.001$). No significant difference was found between the Phaeophyta and Rhodophyta phyla ($p = 0.190$). Figure 5C suggests no significant difference is evident between our 2023 Phaeophyta survey and the wider database. However, our Chlorophyta $\delta^{13}C$ data is slightly depleted in comparison to the database (Fig. 5C) and shows less variation around the mean. The Rhodophyta phyla is most different between our survey and the database, with 2023 plotting significantly higher than the database (Fig. 5C). No clustering of data is evident in our survey for Rhodophyta with only five specimens recording $\delta^{13}C$ values below – 20.0 ‰ (Fig. 5C). Only inter-tidal Rhodophyta and Chlorophyta were sampled in our survey, therefore they do not capture the full spectrum of Antarctic macroalgae.

Of the 60 species in the database, 51 had both $\delta^{13}C$ and $\delta^{15}N$ data (32 Rhodophyta, 11 Phaeophyta and 8 Chlorophyta). Plotting $\delta^{13}C$ against $\delta^{15}N$ reveals a positive correlation between the two isotopes for all phyla (Fig. A1). This trend is also evident in our more limited 2023 survey of six species (Fig. 7). Species show considerably more variation in $\delta^{13}C$ when compared to $\delta^{15}N$ across all phyla (Fig. 5 and 7). There is also a strong bias in phyla towards Rhodophyta and Phaeophyta. The easily identifiable Desmarestiales and *H. grandifolius* are again overrepresented in the database due to the high number of trophic structure publications utilising stable isotope analysis. However, improved identification is required and a greater effort for expanding collection to include Chlorophyta species. As glaciers retreat and new ice-free areas are exposed, opportunistic Chlorophyta will be some of the first to colonise. Therefore, understanding their biogeochemical and ecophysiological properties will be critical in understanding the changing carbon and nutrient dynamics of the Antarctic coastal ecosystem.

3.4.1 Nitrogen ($\delta^{15}N$):

Macroalgal $\delta^{15}N$ varies less than $\delta^{13}C$ and plots over ~ 16 ‰ range (Fig. 4). As with $\delta^{13}C$, Rhodophyta is overrepresented in the database with 301 analyses, but the lack of Chlorophyta is even more pronounced with only 19 database points (Fig. 4B). A lack of samples and misidentification is a problem for the Chlorophyta phylum. The majority of macroalgae $\delta^{15}N$ plots between +2 and +6 ‰ (Fig. 4B), which is typical for the Southern Ocean and reflects a "natural" nitrogen source (DiFiore et al., 2009; Sigman et al., 2000; Stukel and Ducklow, 2017). Phaeophyta and Rhodophyta macroalgae record a lower nitrogen isotope signature compared to Chlorophyta, with some plotting < 0 ‰ (e.g., *H. grandifolius* and *Desmarestia* sp.) (Fig. 5 and 7). Various regions of the Southern Ocean have shown anomalously low $\delta^{15}N$ values (Sigman et al., 2000); potentially reflecting this high nitrate environment (Henley et al., 2017). When in surplus nitrogen concentrations macroalgae will discriminate for ^{14}N over ^{15}N, reducing the $\delta^{15}N$ signature as a result (Ochoa-Izaguirre and Soto-Jiménez, 2015; Sigman et al., 2000; Swart et al., 2014). Elevated ratios may therefore reflect reduced nitrate availability (e.g., from a phytoplankton bloom), whereby macroalgae uptake of ^{15}N is increased due to the smaller N pool and reduced ^{14}N availability (Ochoa-Izaguirre and Soto-Jiménez, 2015; Swart et al., 2014).

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Isotopic variation has been documented for various thallus structures, with holdfasts often recording significantly different values to the rest of the structure (Bebb et al., 2023). The 2023 survey also revealed a depleting trend from meristem to the distal end for *H. grandifolius* across multiple specimens. Variation in nitrogen uptake and growth rates may be affecting this, with assimilation rates slowing at the distal end as photosynthesis rates decline (Bebb et al., 2023; Dyer et al., 2019). More complex macroalgae such as *Cystophaera jacquinotti* or *Desmarestia* sp. may also show similar variation between different morphologies and thallus structures. Although $\delta^{15}N$ shifts are smaller than $\delta^{13}C$, they still have the potential to affect the isotopic baseline as consumers feeding on different thallus structures may record different isotopic ratios despite having the same food source. The nitrogen record is smaller than the carbon, additional analyses are required to improve understanding of species variation and the effect of thallus morphology on shifting baseline values. Additionally, as human influence increases industrial pollution (e.g., detergent from cruise wastewater) has the potential to become a new source of nitrogen for the region with the potential to reduce the isotopic baseline. Antarctica is becoming increasingly popular as a tourist destination, more pollutants may be released and could therefore alter where baseline primary producers receive their nutrients, with the potential for this to be reflected higher up the food chain.

3.4.2 $\delta^{13}C$ — a biological proxy for primary production in macroalgae

Phyla exhibit similar $\delta^{13}C$ ranges from ~ 25 ‰ to ~30 ‰ and all three phyla plot between –20 ‰ and –10 ‰, suggesting most samples use both CO_2 and HCO_3^- for carbon acquisition (Maberly et al., 1992; Raven and Hurd, 2012). Only Phaeophyta and Rhodophyta results show exclusive HCO_3^- uptake (Fig. 4C), with a handful of values plotting > –10 ‰ (Maberly et al., 1992; Raven et al., 1995, 2002). There are almost 200 more Phaeophyta and 300 more Rhodophyta analyses than Chlorophyta. So, whilst Chlorophyta shows a significantly higher $\delta^{13}C$ average (Fig. 4C), indicating a trend towards preferred CCM use, further research is required for Chlorophyta to establish clear trends and baseline values. Many Phaeophyta and Rhodophyta record $\delta^{13}C$ values indicative of CO_2 uptake versus HCO_3^- (Figs. 3 and 4C), implying many Antarctic species utilise passive CO_2 uptake. Raven et al. (2002) identified colder temperatures as a reason for reducing photosynthetic activity and carbon demands for this favouring of passive carbon acquisition and low $\delta^{13}C$ values. The $\delta^{13}C$ average for Phaeophyta and Rhodophyta plot within 1 ‰ of each other, recording no significant difference and suggests most species utilise active HCO_3^- and passive CO_2 uptake (Raven et al., 1995, 2002). The much narrower inter-quartile range for Phaeophyta, confirmed with the lower standard deviation (± 5.6 ‰ to Rhodophyta's ± 8.3 ‰), reflects the low species diversity of the dataset. Only 13 Phaeophyta species have $\delta^{13}C$ results, almost three times less than the number of Rhodophyta species (37), and two thirds of which are *Desmarestia* sp. and *H. grandifolius*. Presence of a CCM, or lack thereof, is species specific (Fernández et al., 2024; Jacobs et al., 2023; Marconi et al., 2011); dominance of *Desmarestia* sp. and *H. grandifolius*, documented to have capacity for both HCO_3^- and CO_2 uptake, would reduce the overall $\delta^{13}C$ variation for Phaeophyta (Iñiguez et al., 2016; Wiencke and Clayton, 1990).

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Whilst Phaeophyta plots relatively evenly across the 30 ‰ range, Rhodophyta is divided into two groups, one around ~ –35 ‰ and then the second between –20 ‰ and –15 ‰ (Fig. 4C). This clustering is only evident from the wider database, our limited 2023 survey of inter-tidal Rhodophyta does not show significantly depleted $\delta^{13}C$ values < –30 ‰ (Fig. 4C). Of the 32 database Rhodophyta $\delta^{13}C$ results, 17 (or 53 %) plots below the –30 ‰ CCM threshold (Fig 4C) (Cornwall et al., 2017; Maberly et al., 1992; Raven and Hurd, 2012). Despite a high proportion of these Rhodophyta being endemic to Antarctica, temperate macroalgae communities also show the same > 50 % proportion of red species relying solely on CO_2 diffusion (Hepburn et al., 2011). Only two Phaeophyta (*Phaeurus antarcticus* and *Microzonia arcta*) and one Chlorophyta (*Lambia antarctica*) show the same extreme negative values (Supplementary Figure 1). Figure 4C shows the second group slightly enriched by ~ 10 ‰, these analyses are from 13 Rhodophyta species that use both CCM and HCO_3^-. Although some individuals plot > –10 ‰ (Fig 4C), no species of any phyla has an enriched $\delta^{13}C$ average > –10 ‰, thus implying all Antarctic macroalgae utilise passive diffusion or a mix of passive and active (CCM) uptake, with the caveat that only 60 of 151 identified species have been analysed for $\delta^{13}C$. With no indication of how many Antarctic species rely solely on HCO_3^- then future response of Southern Ocean macroalgae to ocean acidification cannot be fully realised. Increasing carbon concentrations may benefit species that can downregulate their energetically expensive CCMs in response to CO_2 concentration, energy requirements, and light levels (Cornwall et al., 2012, 2017). Therefore, macroalgae that can only acquire carbon through a CCM may not see any comparative benefit in growth with the predicted future increase in carbon concentration, although they certainly won't be carbon limited (Cornwall et al., 2012, 2017; Iñiguez et al., 2019).

Although individual studies found low intraspecific variation < 2 ‰ (Fischer and Wiencke, 1992; Gillies et al., 2012b); the combined database, and the 2023 survey, show wide $\delta^{13}C$ ranges for some species (*H. grandifolius*, *Desmarestia* sp. and *I. cordata* to name a few) (Fig. 5C). Limited analyses in many studies, sometimes less than five per species, means the full picture cannot be captured with one survey. Intraspecific $\delta^{13}C$, $\delta^{15}N$ and CN is depicted in more detail in Figure 5; the 2023 survey captures greater variation for species with more analyses than the database (e.g., *H. grandifolius* and *M. hariotii*). Whilst the database results for *Desmarestia* sp. shows more detail than our very limited 2023 data (Fig. 5C). Some species occupy a wide variety of ecological niches, and the $\delta^{13}C$ value will therefore fluctuate as a result. Using *H. grandifolius* as an example, intraspecific variation can be explained by its wide depth range and latitudinal coverage. Although Fischer and Wiencke (1992) did not identify any influence of depth on $\delta^{13}C$ for this species, more recent publications report varying $\delta^{13}C$ between location and across depth profiles (Zenteno et al., 2019).

Significant variation is also possible within a single organism, especially for the larger macroalgae species. Michel et al. (2019) was one of the few studies to assess $\delta^{13}C$ variation between different structures, reporting *H. grandifolius* blades had depleted $\delta^{13}C$ values compared to the holdfast and stipe. Morphological variation has received little attention; almost all studies took only one isotope analysis per specimen often labelled as "thallus" or "blade". Intra-blade $\delta^{13}C$ and $\delta^{15}N$ variation has started to be investigated for *Laminariales*; Dyer et al.

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(2019) reports consistent patterns in both isotopes across kelp fronds reflecting changes to growth. No similar scale of study exists for Antarctic macroalgae. Whilst Dunton (2001) states *H. grandifolius* displays no variation along the blade, no information is provided on the interval size or sample number per blade. Only lengths of 150 cm were analysed, this is a relatively short sampling distance for a species that's blades can reach > 10 m in length. Results from several blades collected in December 2024 (Alldred et al., unpublished) revealed up to 15 ‰ variation for one specimen, directly contradicting the Dunton (2001) study. A publication for this is planned next year. Clearly more work is required to understand shifts in isotopic baselines from these larger macroalgae. Thallus isotope variation is complicated, but understanding the baseline variation is critical in understanding the wider food web. Especially where macroalgae detritus forms such a large percentage of the diet of consumers (Ahn et al., 2021; Dunton, 2001; Wiencke and Amsler, 2012). Standardising of the sampling method needs to be established, and ensuring data is available for all thallus structures, as well as multiple analyses for particularly large blades, will reduce error and contribute to understanding grazing and nutrient transfer.

3.4.3 Geospatial Variation:

Spatial variation and trends for macroalgal $\delta^{13}C$ and $\delta^{15}N$ can only be assessed for the WAP region since > 77 % of the data is from here (Fig. 1). Isoplots for Chlorophyta (Fig. 8), Phaeophyta (Fig. 9) and Rhodophyta (Fig. 10) show both data for prior studies and data from this study. Our 2023 survey is concentrated on the Gerlache Strait, an understudied region in terms of macroalgae biogeochemistry (Fig. 1). Chlorophyta shows higher $\delta^{15}N$ values than Rhodophyta and Phaeophyta at the same site (Figs. 8–10). In our survey, site specific variation was evident with a clear ^{15}N enrichment found in Chlorophyta from Yankee Harbour, a large Gentoo penguin colony in the SSI (Fig. 8). Field locations show spatial variation of ~4 ‰ for Chlorophyta $\delta^{15}N$, ranging from < 3.1 ‰ (Iken et al., 2023) to > 7.0 ‰ (Dunton, 2001) and then > 10 ‰ upon inclusion of our data (Fig. 8). However, spatial coverage is poor with much of the database focussed on Anvers Island separated by only a small headland. No clear spatial trend is evident in $\delta^{15}N$, varying by only ~ 8 ‰ across the WAP in both Phaeophyta and Rhodophyta. Over 50 % of sites plot between +3 ‰ and +5 ‰; typical of the Southern Ocean $\delta^{15}N$ signature (DiFiore et al., 2009; Sigman et al., 2000). Nitrogen is elevated > 5 ‰ at only one site for Phaeophyta (Iken et al., 2023) and only two sites for Rhodophyta (King George Island, in Rosenfelder and Vetter (2012) and at Portal Point (this study). Figure 9B indicates Phaeophyta have depleted $\delta^{15}N$ signatures compared to Rhodophyta (Fig. 10B) in the SSI. Site variation is high south of Anvers Island, but again Rhodophyta appear to record $\delta^{15}N$ values ~ 1–2 ‰ higher for many of the Iken et al. (2023) sites. Greater variability in the Rhodophyta phylum could be driven by the higher biodiversity and larger sample set. Interestingly, different species at the same site (e.g., *A. utriculares*) did not show significantly enriched values like in *M. hariotii* (Figs 7 and 8B). Different phyla at the same site show varying $\delta^{15}N$ values for the database (Figs. 8–10); with Phaeophyta often recording significantly lower values than Rhodophyta or Chlorophyta. A differing nitrogen source is unlikely for the same site, especially one where no human infrastructure exists. Instead, species specific differences in nitrogen

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assimilation and uptake rates may be influencing the $\delta^{15}N$ value of certain species. Nitrogen turnover rate is species specific; opportunistic macroalgae often have high nitrogen demands due to a fast growth rate; some can assimilate nitrogen in ~48 hours (Bailes and Gröcke, 2020; Gröcke et al., 2017). A higher nitrogen demand would elevate the $\delta^{15}N$ value as more nitrogen is required. Species with slower growth rates may respond differently, having a lower nitrogen demand, not need to utilise the entire N pool and therefore uptake less ^{15}N. Identifying spatial trends for the Chlorophyta phylum is difficult, the lack of field locations means only broad assessments can be made from the four studies that include this phylum and our limited Chlorophyta survey (Corbisier et al., 2004; Dunton, 2001; Fernández et al., 2024; Iken et al., 2023).

Figures 8–10 shows $\delta^{13}C$ varies between sites for all three phyla, with a latitudinal trend strongest in Rhodophyta. Almost all SSI sites > –26.9 ‰, with the more depleted sites < –33 ‰ south of Anvers Island (Fig. 5C). Spatial variation in both Rhodophyta and Phaeophyta is much more evident due to the higher number of field locations (Figs. 9 and 10). Rhodophyta plot on average ~5 ‰ higher in $\delta^{13}C$ values than Phaeophyta in the SSI. However, this changes further south on the WAP where Rhodophyta is more depleted than Phaeophyta for the same site (Fig. 9 & 10). South of Anvers Island, several sites plot below –30 ‰ for Rhodophyta (Fig. 10A). Phaeophyta $\delta^{13}C$ values are generally between –24 ‰ down to ~ –29.9 ‰. Broad spatial trends are similar between the two phyla, but a stronger correlation between latitude and $\delta^{13}C$ is present for Rhodophyta. The $\delta^{13}C$ signature is somewhat elevated for Chlorophyta compared to the other phyla collected from the same site (Fig. 1); this is most obvious at Anvers Island whereby Chlorophyta is less negative by ~17 ‰. But, the limited dataset for Chlorophyta limits further interpretation. Varying irradiance with latitude has been identified as a strong control on macroalgae growth, productivity and cover (Amsler et al., 2023; Whippo et al., 2024; Iken et al., 2023). Irradiance also has a strong influence on $\delta^{13}C$ in seaweeds (Cornelisen et al., 2007); influencing the downregulation of the CCM for carbon uptake in response to PAR and carbon demand (Gómez et al., 2009; Hepburn et al., 2011; Matula et al., 2022). Passive uptake is less energetically expensive, often utilised where PAR is low, or CO_2 concentrations are sufficiently high (Cornwall et al., 2012). CCMs, on the other hand, are associated more with higher PAR environments (i.e., lower latitudes, low sea ice, or shallower depths) as increased photosynthetic activity means greater carbon demands, therefore increasing HCO_3^- uptake and the $\delta^{13}C$ value of the organism (Fischer and Wiencke, 1992; Maberly et al., 1992). The ecological niche of the species will impact its $\delta^{13}C$ value, light is the underlying factor, but this is influenced by sea ice, depth and latitude (Fernández et al., 2024; Iken et al., 2023; Joy-Warren et al., 2019; Matula et al., 2022). Sub-tidal and inter-tidal macroalgae can therefore have very different $\delta^{13}C$ values, even at similar locations (Fernández et al., 2024; Zenteno et al., 2019).

3.4.4 Temporal Variation: $\delta^{13}C$ as a proxy for sea ice?

The limited dataset for the Southern Ocean means understanding the current isotopic baseline is fractured, with only a clear picture for the SSI (Fig. 1). Monitoring future ecological

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communities and the shifting baseline will become harder if no new surveys are conducted. The poleward shift in species distribution means new ecological communities are likely to establish in newly ice-free areas and higher latitudes (Duarte et al., 2022; Pessarrodona et al., 2019). Spatial variation in both $\delta^{13}C$ and $\delta^{15}N$ is evident across the WAP, new communities are likely to have specific baselines that require new research. Newly ice-free areas at the foot of retreating glaciers may receive more terrestrial nutrient sources driven by meltwater processes. Continued biogeochemical research is needed to establish the various nutrient sources acting on the Antarctic coastal community. Potter Cove (SSI, Fig. 1) is an excellent example of continued biogeochemical monitoring of a changing environment (Weber et al., 2017). But this small bay should not be taken as representative for the entire continent.

Climate change has had a profound impact on the Antarctic ecosystem. Air temperature is warming ~2 ºC per decade (Deregibus et al., 2025); causing instability of ice sheets, glaciers, fast-ice and ultimately the biological community (Oliveira et al., 2020; Pellizzari et al., 2025). Uncertainty in how primary producers will respond to future climate scenarios is high, especially for the Southern Ocean (Pessarrodona et al., 2019; Smale, 2020). Reduced sea ice conditions and warmer temperatures may enhance growth rates or the increased turbidity from melting glaciers could reduce PAR to below the threshold required for some species (Deregibus et al., 2025; Drew and Hastings, 1992). The biological carbon pump is closely tied to sea ice dynamics (both timing and retreat), carbon isotopes may provide a novel approach to monitoring productivity, photosynthetic method and carbon demands (Dittrich et al., 2022; Massom and Stammerjohn, 2010; Stukel and Ducklow, 2017). The $\delta^{13}C$ record fluctuates with changing sea ice extent across the ~35-year record (Sea Ice and Snow Cover Extent, 2026) (Fig. 11). Both the sea ice area and $\delta^{13}C$ phyla averages show low variability prior to 2008, but as the sea ice area fluctuates more over the recent decade so does $\delta^{13}C$ (Fig. 11). Peaks and troughs in the sea ice area show similarities with the timing of $\delta^{13}C$ changes in both Rhodophyta and Phaeophyta. Reduced $\delta^{13}C$ averages coincide with increased sea ice (~ 2013–2014), years with anomalously cold summers and winters (Deregibus et al., 2025; Pellizzari et al., 2025). Reduced carbon demands in low light environments have been correlated with lower $\delta^{13}C$ values (Gómez et al., 2009; Vanderklift and Bearham, 2014; Wiencke and Fischer, 1990); variation in the $\delta^{13}C$ record in Figure 11 may be a result of reduced PAR due to increased sea ice and elevated nutrient concentrations triggered by increased meltwater. Conversely, greater $\delta^{13}C$ values correlate with sea ice decline from ~2016 onwards. This period was also associated with anomalously warm temperatures recorded in the SSI where most of the stable isotope data comes from (Fig. 1) (Deregibus et al., 2025). Longer sea-ice free periods can increase photosynthetic demand in primary producers due to more favourable light conditions, thus raising the carbon demand and the need for increased uptake (Eayrs et al., 2019; Gómez et al., 2009; Joy-Warren et al., 2019). The increased $\delta^{13}C$ values in Figure 11 could reflect this increase CCM use to meet greater carbon demands. Figure 11 highlights the potential for macroalgae biogeochemistry to be utilised beyond trophic ecology and photosynthetic mechanism assessments. Through routine monitoring we highlight the potential for use as an indicator of primary producer response to environmental change on a long-term scale.

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4. Conclusions & Future Considerations:

This review presents the first collation of $\delta^{13}C$, $\delta^{15}N$ and CN data for Antarctic macroalgae collected over a 35-year period between 1987 and 2023. The dataset is bias towards the West Antarctic Peninsula, representing 77 % of all analyses that are concentrated at research bases. We present new data for the peninsula and highlight the potential for collaboration with expedition tour operators to enable research at new field sites away from research bases.

The CN dataset highlights an offset between the global macroalgae CN ratio and the lower Antarctic ratio, likely driven by the higher nitrogen content of polar seaweeds. The $\delta^{15}N$ dataset was found to be less variable than the $\delta^{13}C$ dataset but still showed spatial and species variation. The Rhodophyta phylum, as well as the Phaeophyta *H. grandifolius* and the *Desmarestia* sp. genus are the most well studied for CN, $\delta^{15}N$ and $\delta^{13}C$. However, intra-species variation has been largely ignored and there are fewer than 100 analyses per species. Further research is required to ascertain fluctuation across the growth season, with depth and in response to changing sea ice and temperature conditions. Trophic structure remains the most popular research area for publishing Antarctic macroalgae isotope data, however intra-specimen variation has the potential to propagate up the food chain. Understanding remains poor, many papers included here report only a handful of analyses per species. Finally, when plotted temporally $\delta^{13}C$ shows a previously unexplored link to sea ice extent and primary producer response to increasing instability. Reduced $\delta^{13}C$ values corresponding with reduced sea ice may indicate increased productivity in response to a warming Antarctic climate. In conclusion, Antarctic macroalgal biogeochemistry is a relatively new field of study, with sporadic publication over the past four decades. Regular field surveys across the peninsula, and wider Antarctic continent, could provide valuable insights into ecophysiology, trophic structure, nutrient cycling and productivity in response to the changing Antarctic climate.

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FA carried out all fieldwork, data analysis, initial draft and writing of the manuscript. DG contributed to writing, data analysis, revisions and supervision of the project.

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Data Availability:

The data is available as supplementary material for this manuscript and will also be made available upon request.

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Figure 1

Field locations for all macroalgae $\delta^{13}C$, $\delta^{15}N$ and/or CN data from the Antarctic Continent. Prior studies are represented by blue circles, the 2023 field locations from this study are represented by orange circles. Study IDs shown here are described in the summary data file.

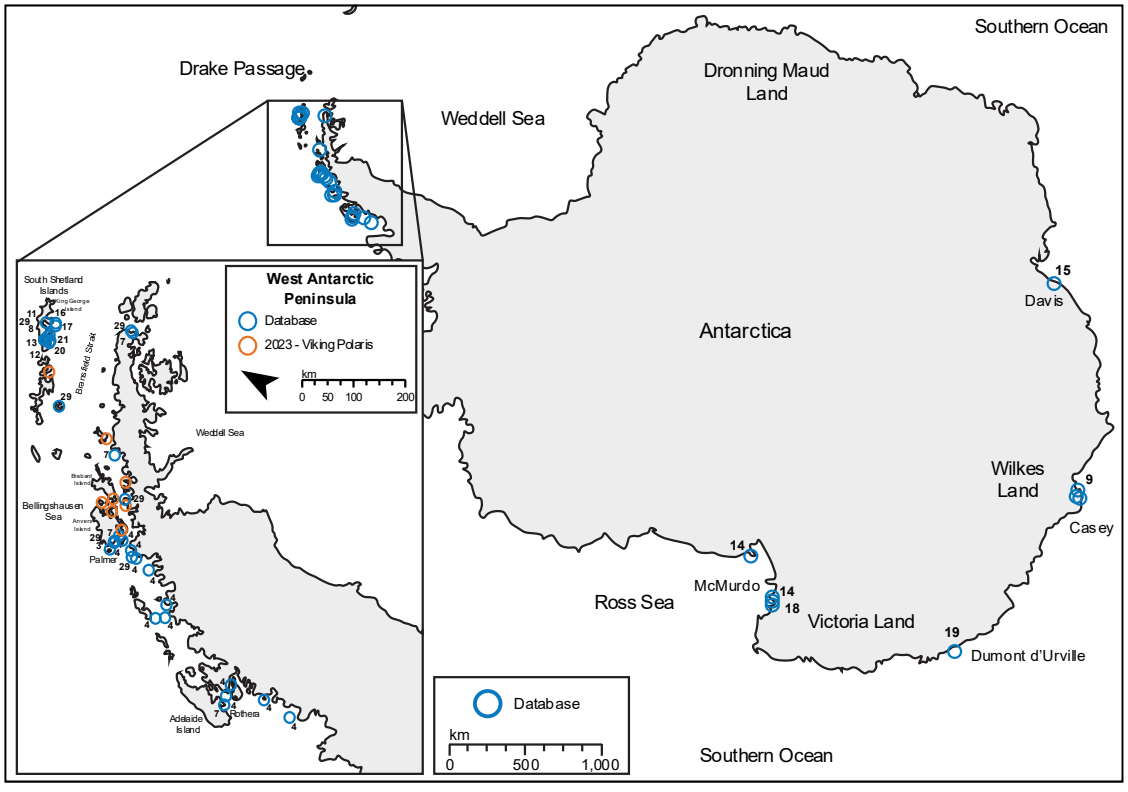

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Figure 2

Timeline of CN (purple), $\delta^{13}C$ (blue) and $\delta^{15}N$ (pink) data entries for Antarctic macroalgae and number of entries. Iken et al., 2023 has the highest number of entries > 250 for $\delta^{13}C$, $\delta^{15}N$ *and* CN. Only four years have all three data types, with studies mostly focussing on either isotope or CN data separately.

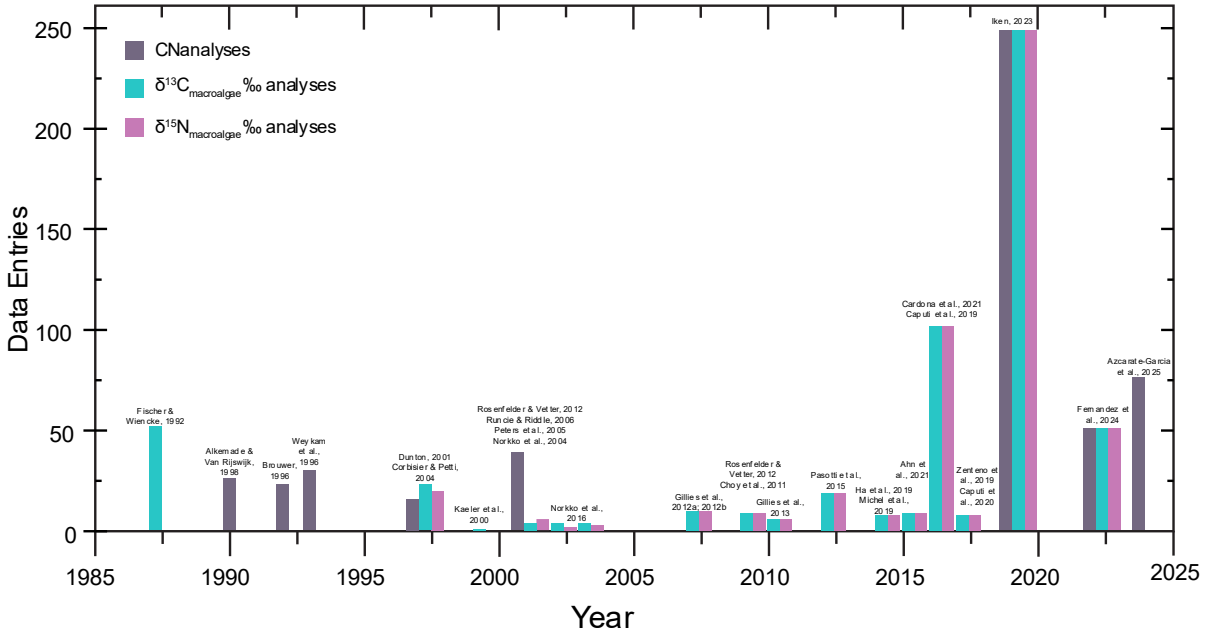

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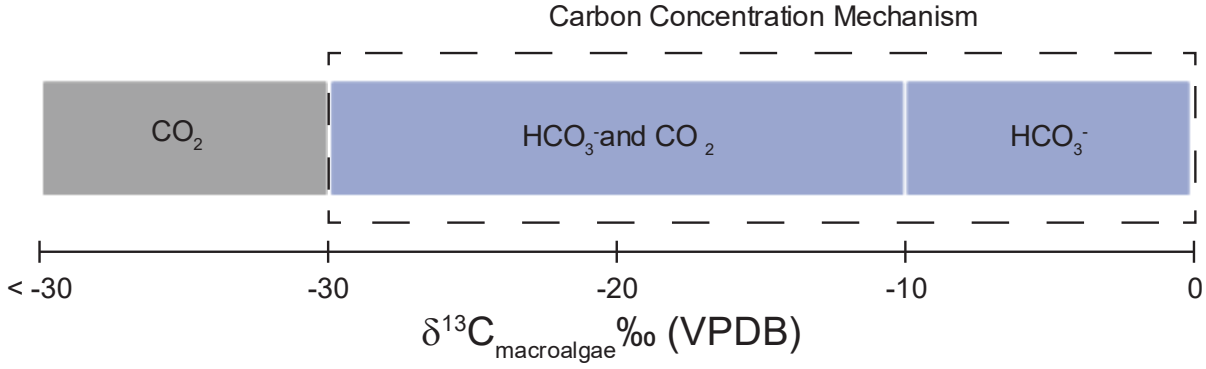
Figure 3

Schematic diagram for carbon acquisition mechanism and macroalgae $\delta^{13}C$ range. A $\delta^{13}C$ value below −30 ‰ indicate passive CO_2 uptake whilst $\delta^{13}C$ values above −10 ‰ indicate HCO_3^- uptake through a carbon concentration mechanism. Values between −30 ‰ and −10 ‰ indicate the macroalgae as capable of using both mechanisms.



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1199 **Figure 4**

1200 All database entries collated into boxplots divided by phylum for CN (A), $\delta^{15}N$ (B) and $\delta^{13}C$
1201 (C) for Chlorophyta (green), Phaeophyta (brown) and Rhodophyta (red).

1202

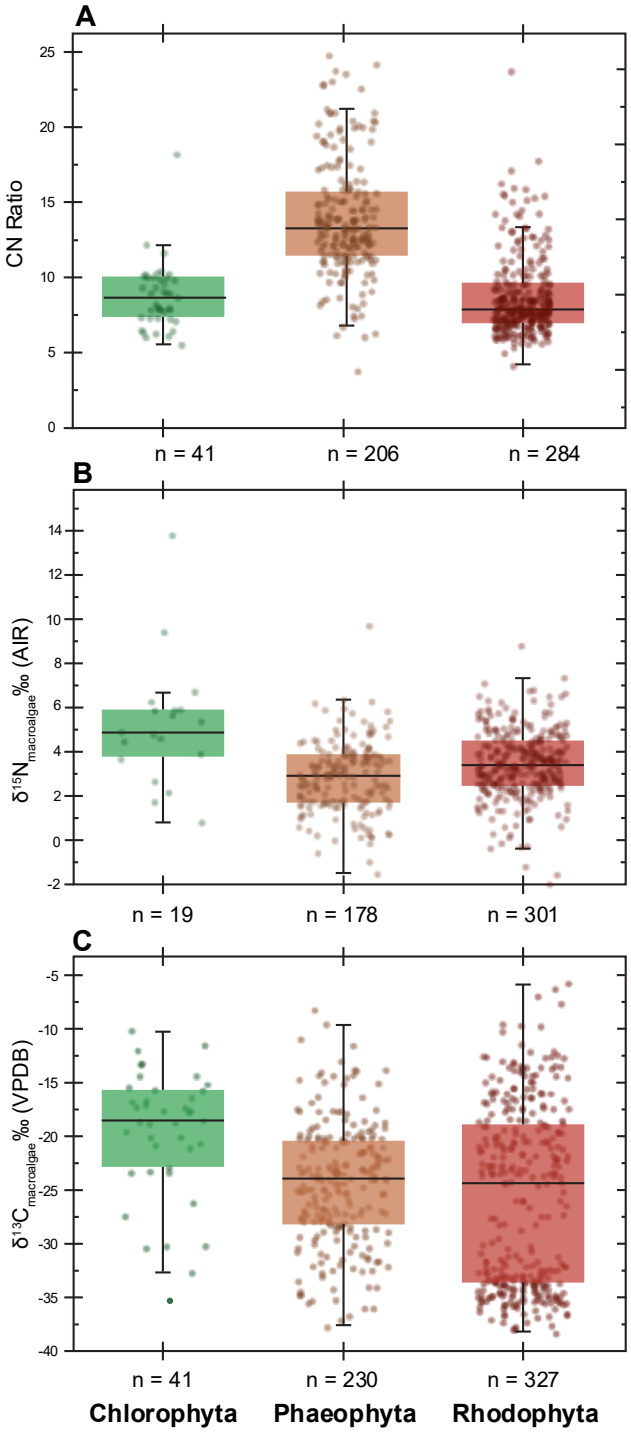

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Figure 5

Boxplots for CN (A), $\delta^{15}N$ (B) and $\delta^{13}C$ (C) comparing species from the database (left) and the 2023 survey from Viking Polaris (right). Some species record no difference between the overall database and 2023 survey (e.g., *Palmaria decipiens*) whilst others show marked differences (e.g., *Iridaea cordata*).

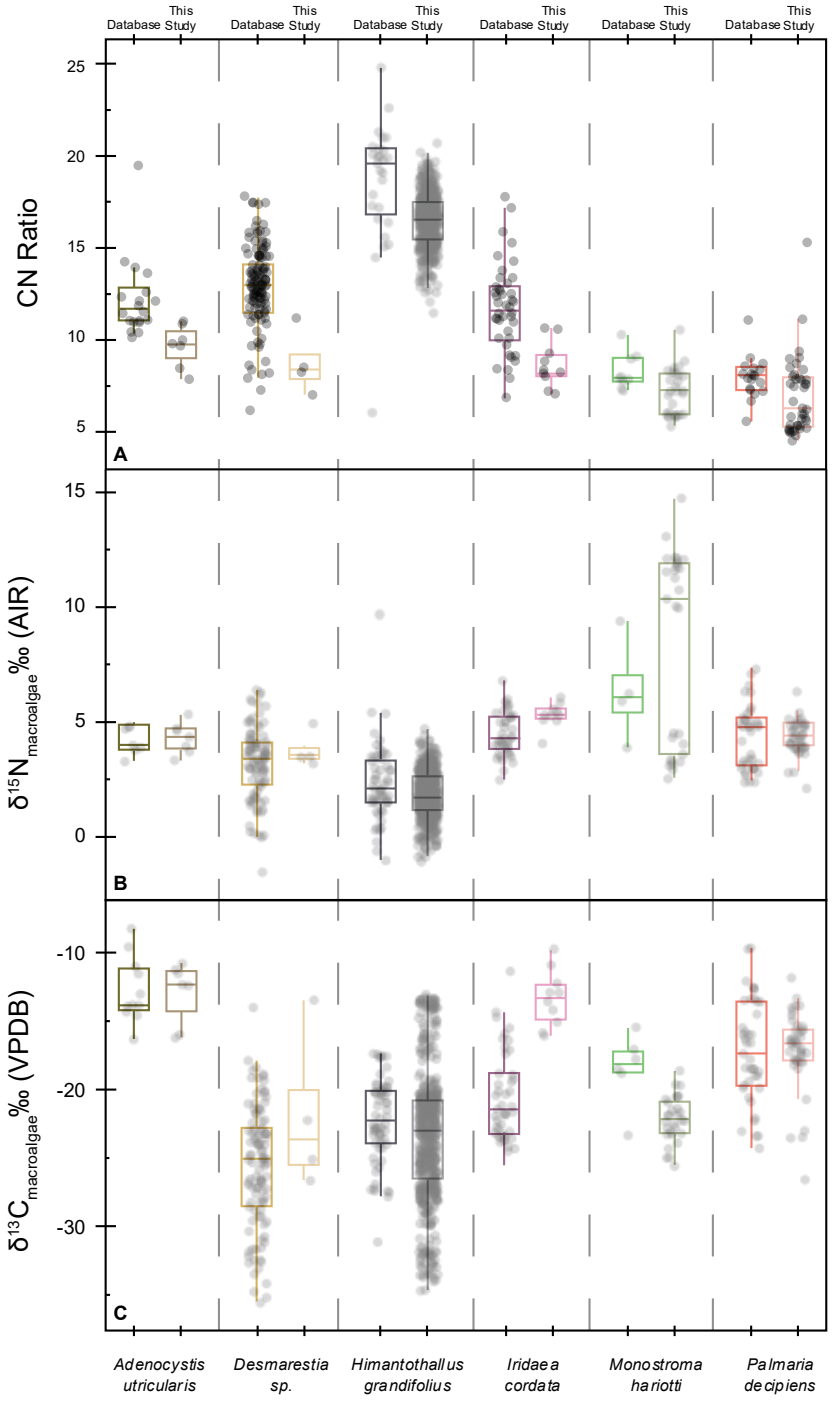

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Figure 6

Carbon plotted against nitrogen content for the database entries (A) showing a positive correlation between increasing carbon and nitrogen content. The 2023 dataset (B) is shown overlain onto the database trend showing a broadly similar pattern, although both Rhodophyta and Chlorophyta shown higher nitrogen contents.

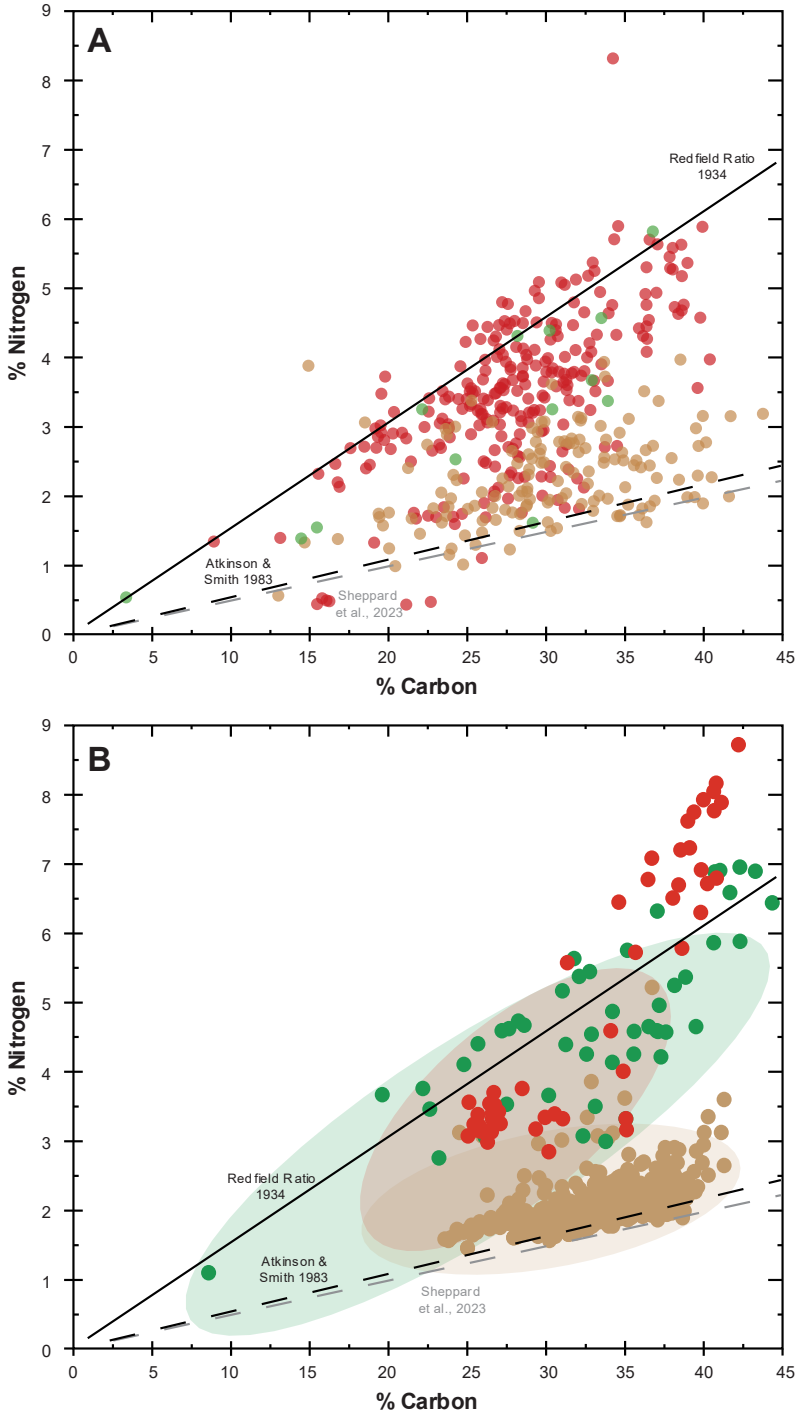

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Figure 7

Comparison between the database (circle) and this study's data (square) for the six species collected in 2023. A positive correlation between $\delta^{13}C$ and $\delta^{15}N$ was found for the database and was also replicated in the 2023 survey.

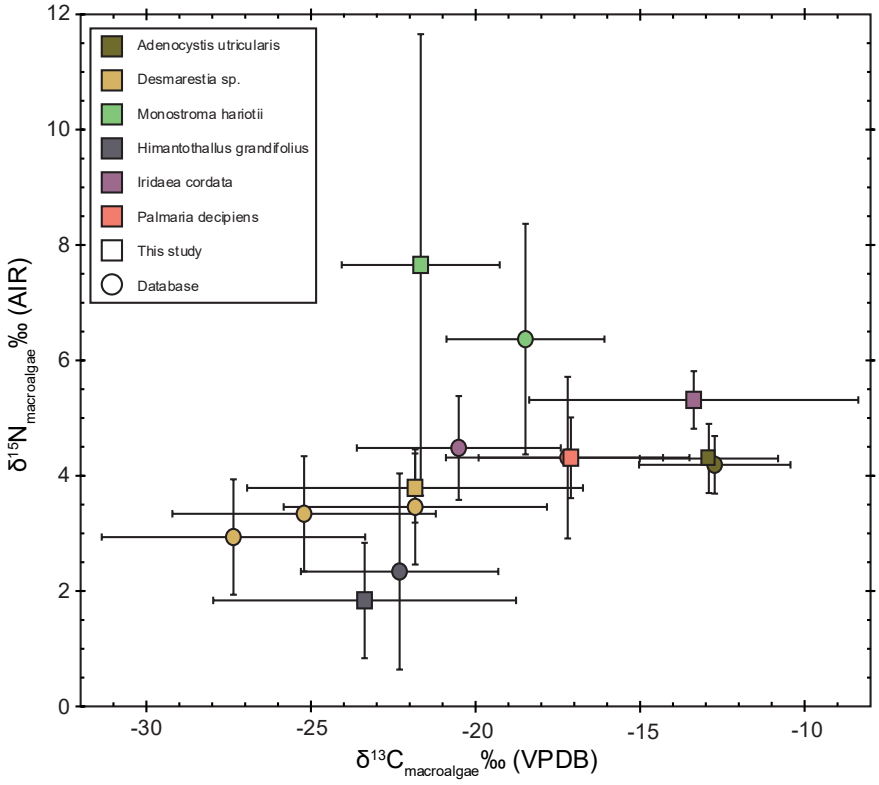

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Figure 8

Spatial variation recorded by Chlorophyta at field sites for the West Antarctic Peninsula for $\delta^{13}C$ (A) and $\delta^{15}N$ (B). Isotopic analysis for Chlorophyta exists for only ten locations (four of which were from 2023) and highlights the lack of research into this phylum in Antarctica.

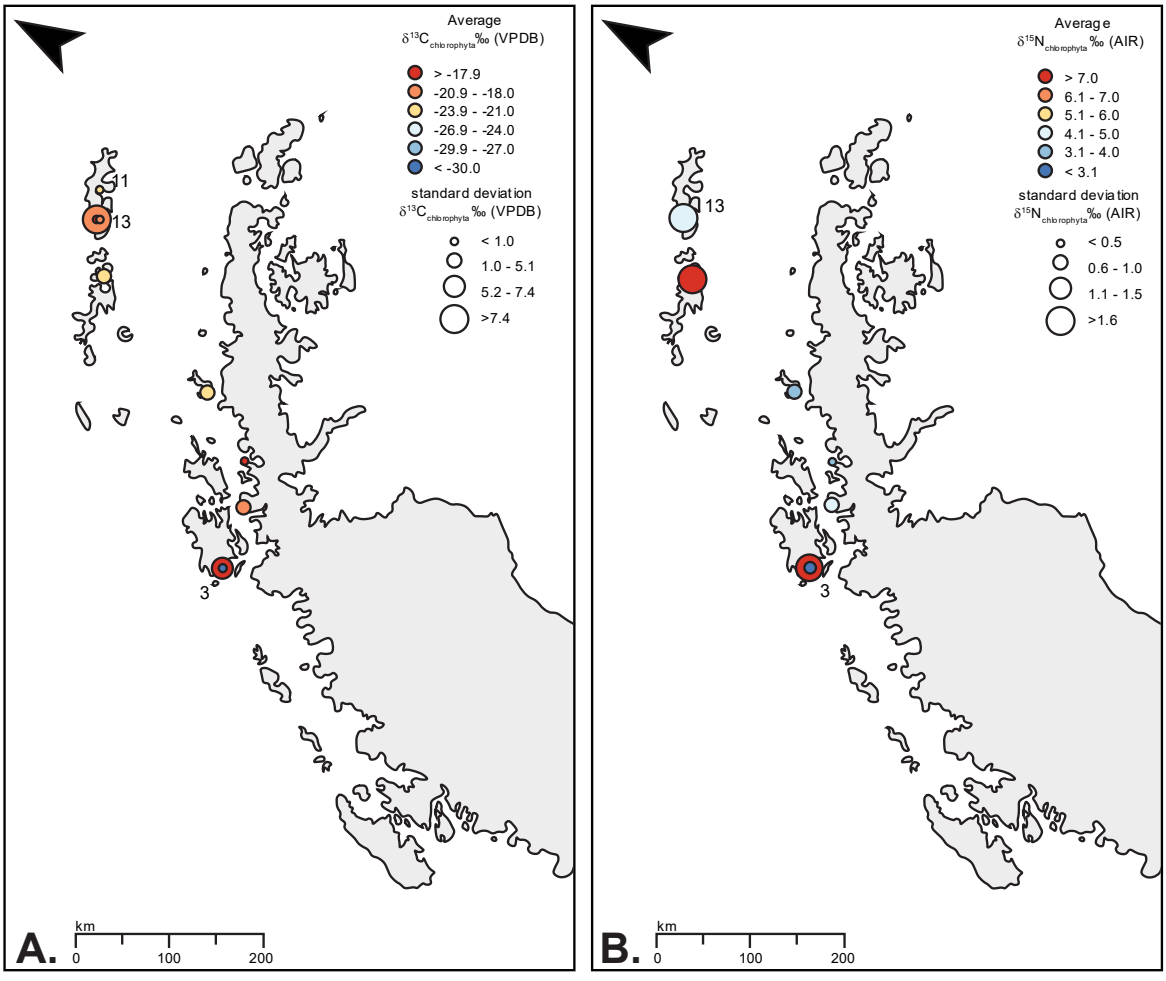

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Figure 9

Spatial variation recorded by Phaeophyta at field sites for the West Antarctic Peninsula for $\delta^{13}C$ (A) and $\delta^{15}N$ (B). Note the greater spatial coverage for this phylum, largely driven by field sites from Iken et al. (2023).

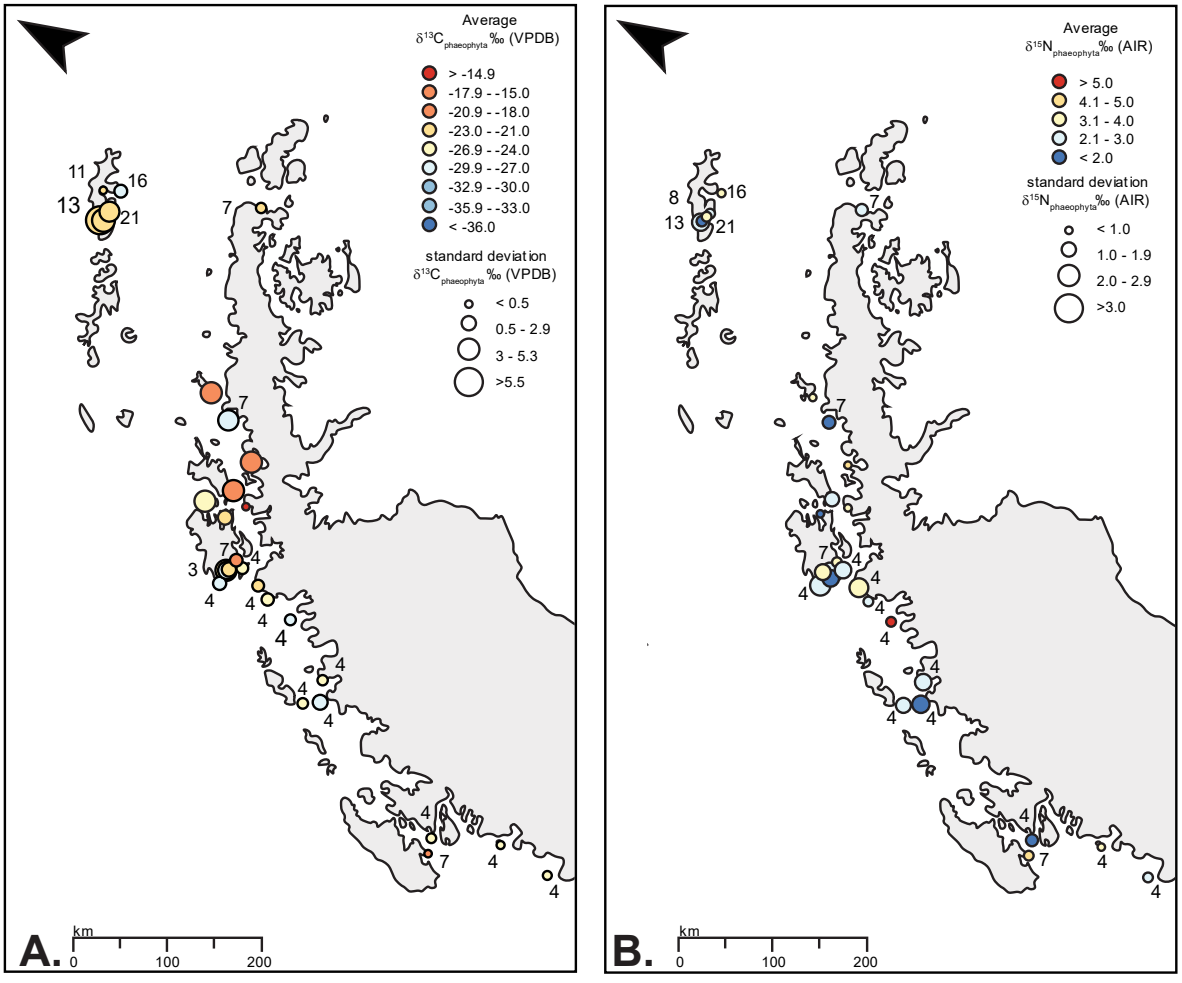

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Figure 10

Spatial variation recorded by Rhodophyta at field sites for the West Antarctic Peninsula for $\delta^{13}C$ (A) and $\delta^{15}N$ (B). Note the greater spatial coverage for this phylum, largely driven by field sites from Iken et al. (2023) and more obvious trend for declining ^{13}C with latitude.

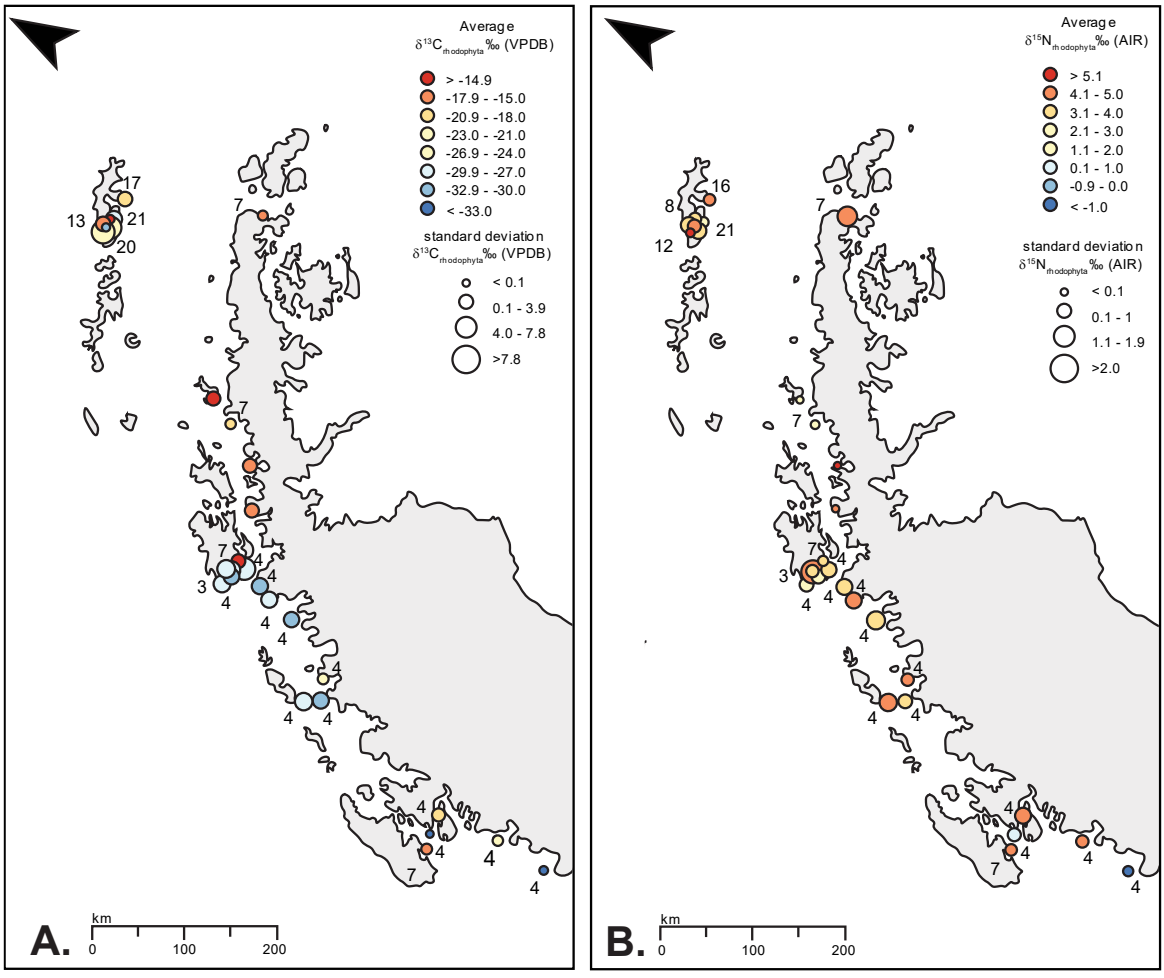

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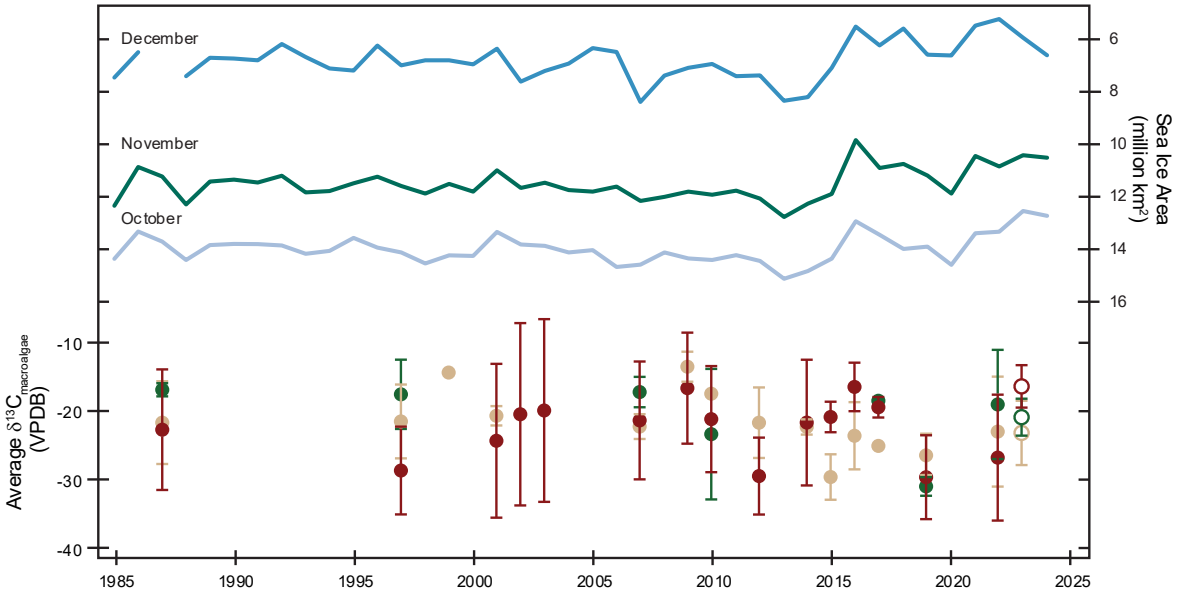
Figure 11

Temporal variation in macroalgal $\delta^{13}C$ plotted across a 35-year period and inclusion of this survey (hollow circle) split by phylum and compared to sea ice extent (million km^2) (National Snow and Ice Data Centre, 2026). Note the reversal of the y-axis for sea ice extent to better highlight the increasing variability and correlation with more negative $\delta^{13}C$ values within the last decade. October–December correlate with the primary growth period of most Antarctic macroalgae.



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Appendix A

Figure A1

Correlation between δ13C and δ15N for each phylum: Rhodophyta (A), Phaeophyta (B) and Chlorophyta (C)