



Macroalgal input into the coastal food web along a gradient of seasonal sea ice cover along the Western Antarctic Peninsula

Katrin Iken^{1,*}, Charles D. Amsler², Kristen B. Gorman¹, Andrew G. Klein³, Aaron W. E. Galloway⁴, Margaret O. Amsler², Sabrina Heiser^{2,6}, Ross Whippo⁴, Alexander T. Lowe⁵, Julie B. Schram^{4,7}, Zoe X. Schneider¹, James B. McClintock²

¹College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA

²Department of Biology, University of Alabama at Birmingham, Birmingham, Alabama 35233, USA

³Department of Geography, Texas A&M University, College Station, Texas 77843, USA

⁴Department of Biology, University of Oregon, Charleston, Oregon 97420, USA

⁵Tennenbaum Marine Observatories Network, Smithsonian Institution, Edgewater, Maryland 21037, USA

⁶Present address: Marine Science Institute, University of Texas at Austin, Port Aransas, Texas 78373, USA

⁷Present address: Department of Natural Science, University of Alaska Southeast, Juneau, Alaska 99801, USA

ABSTRACT: Coastal food webs that are supported by multiple primary producer sources are considered to be more stable against perturbations. Here, we investigated how declining macroalgal abundance and diversity might influence coastal food web structure along an annual sea ice cover gradient along the Western Antarctic Peninsula (WAP). The most common benthic invertebrate consumers, macroalgae, and surface particulate organic matter were collected at 15 stations along the WAP. Stable carbon and nitrogen isotope values of primary producers changed negligibly in relation to the sea ice cover gradient, while isotope values of most invertebrate feeding groups increased with higher sea ice cover, although at low explanatory power. Food web length became shorter and consumer trophic niche width smaller in regions with higher sea ice cover. Changes in food web structure were mostly associated with shifts in trophic position of lower trophic levels. Food web structure in higher ice-covered regions resembled that of more generalist feeders with a loss of specialist species, concurrent with an increased reliance on a more reworked detrital food source. These results suggest that a number of benthic invertebrates are able to adjust to differences in basal energy sources. Conversely, these food webs dominated by generalist feeders are likely less efficient in energy transfer, which can create less-stable systems with lower adaptive capacity to disturbance. The predicted sea ice loss along the WAP may ultimately lead to a longer food web with higher macroalgal abundance, more specialist species, and wider consumer trophic niches in the currently more ice-covered regions.

KEY WORDS: Invertebrates · Stable isotope · Trophic structure

1. INTRODUCTION

Food web theory contends that the use of multiple energy pathways will stabilize food webs because of the complementarity of multiple primary producer sources to provide energy to consumers, especially

where the sources differ in size, growth rates, nutritional quality, and biomass turnover (Huxel et al. 2002). Any fluctuations in the availability of one primary producer, such as from seasonal patterns or disturbance events, could be compensated for in the food web with the increased use of another source.

*Corresponding author: kbiken@alaska.edu

An excellent example for this in coastal ecosystems is the use of both phytoplankton-based and macroalgal-based trophic pathways, in which suspension and detrital feeders can rely on seasonal phytoplankton production or on detrital particles of longer-lived macroalgae that enter the food web when macroalgae senesce (McMeans et al. 2013, Renaud et al. 2015). The use of both energy sources leads to the coupling of strong and weak trophic interactions (McCann et al. 1998). Strong interactions allow for highly efficient energy transfer among trophic levels (TLs), also referred to as 'fast channels', but depend on a consistent supply of the food source. An example of such a fast channel is the use of phytoplankton to support food webs, based on their fast growth rates, high biomass turnover, and small sizes (Rooney & McCann 2012). In contrast, weak interactions are less efficient in energy transfer and are associated with 'slow channels' based on food sources that have slow growth rates, slow turnover, and larger sizes (Rooney & McCann 2012). Macroalgae are an example of comparatively slower channels in the coastal ecosystem, especially in systems where terrestrial input is low, which would be an even slower channel (Elliott Smith et al. 2021). The combination of these fast and slow channels in a system buffers the food web from strong fluctuations based on the availability of the different producer types.

The increase in coastal food web stability through the coupling of multiple energy pathways is particularly important in high-latitude systems where strong seasonality limits phytoplankton production to an intense but short-duration period (e.g. Smith et al. 2000, Leu et al. 2011). The use of more consistently available food sources such as longer-lived macroalgae could become especially important in those high-latitude systems. In fact, this concept has been supported in numerous locations in the Arctic and subarctic, showing the coupling of phytoplankton- and macroalgal-based pathways (e.g. McMeans et al. 2013, Siegert et al. 2022), e.g. in systems where strong freshwater influx from land-terminating glaciers can limit phytoplankton production (Hopwood et al. 2020). In the high Arctic, the coupling of phytoplankton and macroalgal pathways could be traced all the way into higher TL fish, supporting the notion that the combination of multiple food sources is important for the larger food web, not simply primary consumers (McMeans et al. 2013). Similarly, in Chilean kelp forests, lower TL consumers preferred either phytoplankton or macroalgal pathways but with individual variability, and these pathways were

linked at higher TLs (Elliott Smith et al. 2021). Less is known about the importance of these processes and coupling of energy pathways in the coastal waters surrounding the Antarctic continent, although the use of a detrital food bank from phytoplankton bloom deposits (Cardona et al. 2021) and slow-degrading macroalgal deposits (Norkko et al. 2004) have been suggested to infer food web stability in the Southern Ocean.

Macroalgae are a common, and often dominant, component of several Antarctic coastal regions (Oliveira et al. 2020). Best studied are the macroalgal stands along the northern part of the Western Antarctic Peninsula (WAP) (e.g. Amsler et al. 1995, Brouwer et al. 1995, Klöser et al. 1996, Wiencke & Clayton 2002). These macroalgal stands can be very high in biomass, even rivaling temperate kelp forests in standing stock (Valdivia et al. 2015, Quartino et al. 2020). Macroalgae are common from just below the ice scour zone at about 5 m to at least 40 m depth (Amsler et al. 2023). Macroalgal communities are dominated in biomass by large brown algae (mostly within the Desmarestiales) but in species diversity by red algae (Wulff et al. 2009). Macroalgae are a known food source for shallow-water consumers in the Southern Ocean (Dunton 2001, Momo et al. 2020). Macroalgae can enter the food web through direct grazing or browsing by lower TL grazers (Iken 1999, Huang et al. 2006, Aumack et al. 2017) or larger omnivores such as coastal fishes (Iken et al. 1997, Barrera-Oro et al. 2019), even though many Antarctic macroalgae contain chemical defenses against grazers (Amsler et al. 2020). Another pathway for macroalgae to enter the food web is as detritus after blade material sloughs off during senescence, and these macroalgal fragments are taken up by a wide variety of different consumers and feeding types (Corbisier et al. 2004, Norkko et al. 2004, Tatián et al. 2008).

Amsler et al. (2023) recently investigated the abundance of macroalgae in the poorly studied southern portion of the WAP, south of Anvers Island (64.5° S). Macroalgae were abundant and diverse to about 66° S, while in the southern-most portion of the study region (to 68.7° S), macroalgal cover was <10% and only contained 2–4 species. Macroalgal cover strongly correlated with the mean annual sea ice cover, presumably with light limitation being the main driver of the reduced macroalgal abundance (Amsler et al. 2023). Here, we aimed to assess the role of macroalgae in the coastal food web along this same sea ice cover/latitudinal gradient, determining if there may be changes in the use of macroalgal-derived carbon

in nearshore invertebrate consumers along this gradient. This idea of latitudinal changes in food web structure in Antarctic coastal systems is not a new one. However, for the most part, the primary producer sources investigated along such gradients have typically focused on the role of sea ice algae in comparison to pelagic phytoplankton production (e.g. Rossi et al. 2019, Caputi et al. 2020). Several studies have also investigated the specific role of macroalgae in the coastal food web in specific locations, e.g. along the WAP (e.g. Dunton 2001, Zenteno et al. 2019, Cardona et al. 2021) and in Eastern Antarctica (e.g. Gillies et al. 2012, 2013, Michel et al. 2019). Of specific note is a recent study investigating the latitudinal changes, from the northern tip of the WAP (Fildes Bay) to Rothera Point, of macroalgal and suspended particulate organic matter (POM) contributions to the coastal benthic food web (Cardona et al. 2021). The partial overlap in sampled taxa, comparable methods, and some spatial overlap of the southern extent of that study with the northern extent of our study here provides a unique complementary view on the importance of macroalgae along a latitudinal gradient on the WAP, representing an important sea ice cover gradient.

We used stable carbon and nitrogen isotope composition to investigate the trophic linkages between common benthic invertebrate consumers of various feeding types with those of common macroalgae and POM, as a proxy for phytoplankton. Stable isotope analysis of bulk carbon and nitrogen ratios of consumer tissues is a common approach to discern the contributions of multiple primary producer (end-member) pathways to the diet of consumers, if these producers have sufficiently different isotope values (France 1995, Peterson 1999, Raven et al. 2002). Carbon stable isotope ratios of different endmembers are preserved with minimal fractionation ($\sim 1\text{‰}$) between TLs (DeNiro & Epstein 1978, Caut et al. 2009). In contrast, a distinct stepwise enrichment in bulk stable nitrogen isotope values between subsequent TLs makes this marker particularly useful in analyzing vertical food web structure, i.e. TLs (Perkins et al. 2014, Jennings & Van Der Molen 2015). Based on carbon sequestration techniques and body size, which determine diffusive exchanges, different primary producers can be distinguished by their carbon stable isotope values. Phytoplankton stable isotope values can be variable, depending on the specific species composition, with added variability in POM from the number of heterotrophic organisms within the mixture, as well as detrital material contributions, all of which influence stable isotope values

(Lee et al. 2004, Lowe et al. 2014). Macroalgae typically have higher carbon stable isotope values, i.e. enriched in ^{13}C , compared with phytoplankton (Peterson 1999). However, depending on the specific carbon-concentrating mechanisms, some red algal species can also be extremely depleted in ^{13}C , potentially resulting in a wide range of carbon isotopic values covered by a macroalgal community. In addition to these systematic differences, the stable carbon isotope value of Antarctic macroalgae can also be influenced by light availability (Wiencke & Fischer 1990), which under field conditions is strongly dependent on sea ice cover. As such, shifting baselines of primary producer stable isotope values may occur and need to be carefully considered when assessing the role of macroalgae in coastal food webs along a large latitudinal or sea ice cover gradient.

The overarching goal of this study was to evaluate if energy sourcing from macroalgae would decrease in coastal invertebrate consumers in more southern regions of the WAP where longer average annual sea ice cover seems to limit the abundance of macroalgae. Would such a change in energy flow also be reflected in a change in trophic structure? It could be reasonable to predict that invertebrates in regions with more limited primary production sources would feed at a higher TL (as indicated by stable nitrogen isotope values; Peterson & Fry 1987, Post 2002), based on increased trophic steps due to microbial processing (Iken et al. 2010).

2. MATERIALS AND METHODS

2.1. Field collections

Sampling was conducted from aboard the ARSV 'Laurence M. Gould' between 23 April and 18 May 2019. Macroalgae and benthic invertebrates were collected at 15 sites along the WAP, from the Anvers Island region (64.59°S , 64.36°W) in the north to the Marguerite Bay region (68.69°S , 67.52°W) in the south (Table 1, Fig. 1). Sites were chosen to be similar in turbidity, derived from the January–March seasonal means from the Visible Infrared Imaging Radiometer Suite (VIIRS) $\text{Kd}(490)$ product (following Wang et al. 2017) and were characterized by their annual (12 mo) mean sea ice concentrations for the weekly National Ice Center (NIC) Ice Charts from 2015 to 2018. Sites were similar in having distinctly sloped topography without being dominated by

Table 1. Details of sites at which macroalgae and invertebrate taxa were collected for stable isotope analysis. Site descriptors also include the average annual sea ice cover extracted from National Ice Center (NIC) ice charts from a 5 yr average (2014–2019), average macroalgal cover, and total number of macroalgal species encountered at each station from video transects (see Section 2 for details); nd: not determined

Site	Latitude (°S)	Longitude (°W)	Date sampled	NIC ice cover (%)	Macroalgal cover (%)	Macroalgal spp. richness
A	–64.7719	–64.3699	15 May 2019	37.3	72.5	23
B	–64.7792	–64.0441	17 May 2019	41.1	79.7	26
C	–64.7932	–64.0072	14 May 2019	41.1	75.5	17
D	–64.9002	–63.8531	10–13 May 2019	36.1	56.0	20
E	–65.1043	–64.0471	7–8 May 2019	53.5	27.7	16
F	–65.2402	–64.2309	18 May 2019	62.9	52.7	20
G	–65.5131	–64.4203	5 May 2019	74.0	11.5	22
H	–65.9449	–66.0249	23 April 2019	56.4	29.2	14
I	–66.0251	–65.3533	16 May 2019	76.8	0.8	7
J	–66.0894	–65.8386	4 May 2019	58.4	6.3	18
K	–66.8773	–67.5752	2 May 2019	82.9	0.0	0
L	–67.5488	–67.7714	30 April 2019	57.9	6.2	4
X	–67.5567	–67.2472	27 April 2019	71.5	nd	nd
M	–68.1758	–67.2682	28 April 2019	68.6	6.1	4
N	–68.6921	–67.5269	29 April 2019	87.7	0.2	2

steep walls. Sites were designated A through N following a general north to south gradient, except for Site X, which was an additional, shallow site with relatively flat topography only sampled for the biomarker work of our larger project (Fig. 1, Table 1). For a detailed description of sites and the selection process, see Amsler et al. (2023).

Each site was sampled using SCUBA transects for an estimate of macroalgal percent cover and of macroinvertebrates between 5 and 40 m (see Amsler et al. 2023). Macroalgal and macroinvertebrate species common to the entire study region, as well as macroalgal and consumer species that were particularly abundant at each site, were hand-collected during SCUBA dives. These samples were obtained mostly from the depth at which they were particularly common at each site, but samples for stable isotope analysis were not collected in a depth-stratified manner. In addition, smaller mesoinvertebrates such as amphipods were collected at each site using an airlift sampler from vegetated and unvegetated seafloor areas and by enveloping one large *Desmarestia menziesii* plant in a fine-mesh bag (Huang et al.

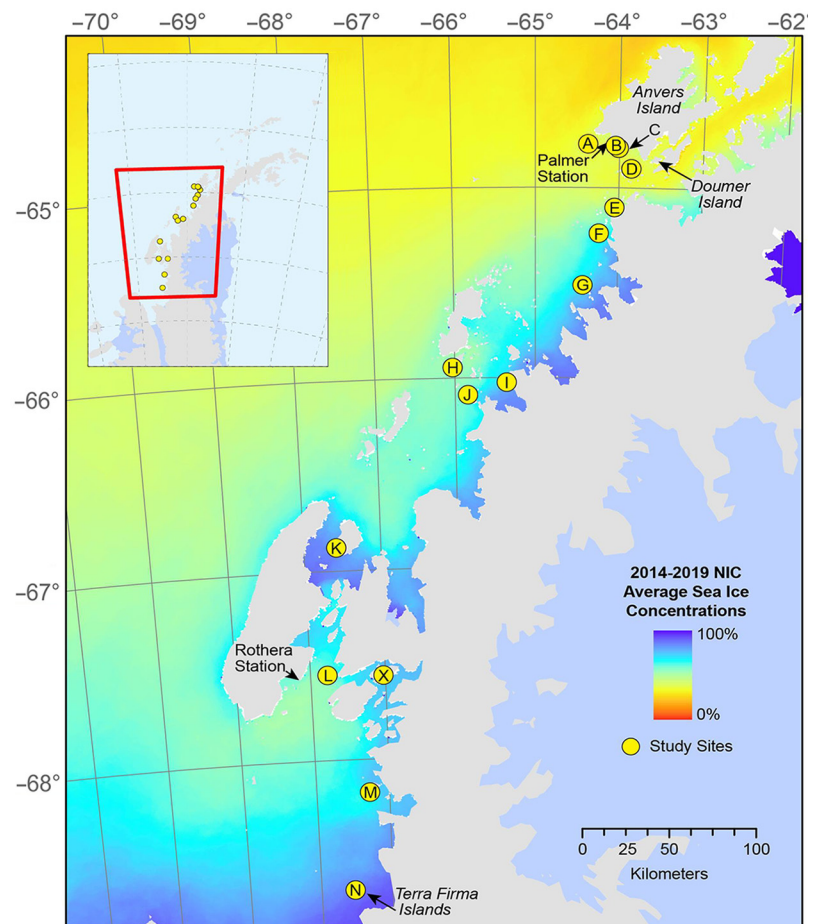


Fig. 1. Study locations along the Western Antarctic Peninsula (inset shows a larger view of the Antarctic Peninsula). Land masses are in gray, with glaciers in light blue. Ocean parts are colored according to the legend by annual average sea ice cover (NIC: National Ice Center). See Table 1 for details

2007). *D. menziesii* was chosen for these bag collections, as we expected it to be present throughout the study area range and because it is known to provide 3-dimensional habitat to an especially large variety of amphipods that typically associate with macroalgae along the WAP (Iken 1996, Huang et al. 2007), providing a means to collect sufficient amphipod biomass and diversity that would not typically inhabit the airlift-sampled seafloor. At 4 sites (B, E, G, and I), benthic microalgae were clearly visible as mats on otherwise unvegetated, soft sediments and were carefully collected as surface scrapes.

On board the research vessel, samples were identified to the lowest possible taxonomic level in the field (usually species or genus) (see Tables 2 & 3). Uncertain taxon identifications were confirmed by our group at the home lab, when possible, and asteroid identifications were kindly confirmed by Dr. Christopher Mah (Smithsonian National Museum of Natural History). Taxon names were standardized according to the World Register of Marine Species (WoRMS, <https://www.marinespecies.org>). Specific thallus portions of macroalgae were selected for analysis, with a focus on branch tips in branched species, middle blade sections in sheet-like species, or whole thalli in particularly small individuals (Table S1 in the Supplement at www.int-res.com/articles/suppl/m718p001_supp.pdf). Thalli were cleaned of debris or fouling organisms by wiping with tissue paper (Kimwipes®) or gently scraping with a razor blade. For the invertebrates, we targeted muscle tissue to obtain tissue comparable in turnover time. In cases where muscle tissue could not be isolated, body wall tissue was used, or complete organisms when they were too small for subsampling. In those cases, gut content was removed when possible (Table S2). Three replicate samples from different individuals were collected for each taxon, depending on availability. POM samples were collected at each site (except for Sites H and L), at least 500 m offshore of the collection coastal site to reduce coastal influences from macroalgal detritus. Up to 6 Nalgene bottles (1 l capacity) of surface waters were collected over the side of a rubber skiff away from the larger research vessel and immediately transported back to the research vessel. There, water samples were filtered as 3 replicates of 800–2000 ml each over 25 mm GF/F Whatman® filters, depending on coloration of the filter and water sample availability. Filters were frozen at –20°C and stored in small petri dishes. All samples (macroalgae, benthic microalgae, invertebrates, POM) were dried in batches in a drying oven at 60°C until constant weight, at least 24 h.

2.2. Laboratory processing

At the University of Alaska Fairbanks (UAF) home laboratory, dried samples were processed for the analysis of carbon and nitrogen stable isotopes. Variable lipid content in invertebrate samples can lead to biases in isotope values, as different fractionation during lipid synthesis can lead to depletion of the ¹³C isotope (Post et al. 2007, Mintenbeck et al. 2008). Therefore, 1 sample replicate from each invertebrate taxon was selected from each site at which they occurred, homogenized, and divided into 2 parts. Lipids were chemically extracted from one part of each of these samples while the other remained untreated. The partial samples selected for chemical extraction were soaked at least 3 times in 2:1 chloroform:methanol (v:v) for at least 12 h for each soak. Solvents were removed and discarded after each soak. After the final soak, samples were re-dried as described above. Any invertebrate samples that contained calcium carbonate (e.g. whole amphipods, tube feet from asteroids) were treated with 1 N HCl by adding the acid drop by drop to the sample until bubbling stopped (Jacob et al. 2005). The acid was then removed, and the sample was rinsed with DI water and re-dried as described above. POM filter samples were exposed to concentrated HCl fumes for 12 h to remove carbonates prior to analysis.

All dried macroalgal and invertebrate samples were homogenized to a powder, and their carbon and nitrogen stable isotope composition was determined at the Alaska Stable Isotope Facility (ASIF) at the Water & Environmental Research Center at UAF using continuous-flow isotope ratio mass spectrometry. This method utilizes a Thermo Scientific Flash 2000 elemental analyzer and Thermo Scientific ConFlo IV interfaced with a Thermo Scientific DeltaV^{Plus} mass spectrometer. Surface material from the POM filters, approximately 0.8–1.2 mg macroalgal material, and approximately 0.3 mg invertebrate tissue were used for the analyses. Results are expressed as conventional δ notation in parts per thousand (‰) according to the following equation:

$$\delta X (\text{‰}) = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000 \quad (1)$$

where X is ¹³C or ¹⁵N of the sample and R is the corresponding ¹³C:¹²C or ¹⁵N:¹⁴N ratio. Pee Dee Belemnite and atmospheric N₂ served as standards for carbon and nitrogen, respectively. Instrument error at ASIF was <0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

2.3. Data analyses

The effect of chemical lipid extraction was evaluated by assessing the C:N ratios of all invertebrate samples; samples with C:N ratios >3.5 are commonly considered to be of high lipid content that would significantly bias the $\delta^{13}\text{C}$ values of the sample (e.g. Post et al. 2007). Many C:N ratios of our non-extracted samples were sufficiently above 3.5 to warrant the evaluation of lipid correction approaches. We used 3 different published mathematical models that are often applied to benthic invertebrates to arithmetically correct the $\delta^{13}\text{C}$ values of the non-extracted sample portion. Briefly, the mathematical corrections ($\delta^{13}\text{C}'$) of the non-extracted $\delta^{13}\text{C}$ values were done using the following equations.

First, per McConnaughey & McRoy (1979):

$$\delta^{13}\text{C}' = \delta^{13}\text{C} + D [-0.207 + 3.90/(1 + 287/L)] \quad (2)$$

$$L = 93/[1 + (0.246 \times \text{C:N} - 0.775)^{-1}] \quad (3)$$

where D is assigned a value of 6‰ as the average isotopic difference between protein and lipid, and L is the calculated lipid content of the sample based on the C:N ratio of the non-extracted sample.

Next, per Alexander et al. (1996):

$$\delta^{13}\text{C}' = \delta^{13}\text{C} + 6 \times (L/100) \quad (4)$$

where L is the lipid content according to Eq. (3), and 6‰ is the average isotopic difference between protein and lipid as in Eq. (2).

Last, per Post et al. (2007):

$$\delta^{13}\text{C}' = \delta^{13}\text{C} - 3.32 + 0.99 \times \text{C:N} \quad (5)$$

Once the final data set with the 3 mathematically corrected $\delta^{13}\text{C}'$ consumer values was created, we compared these mathematically corrected values to the chemically extracted values of the same sample using linear regression. Based on regression fit (R^2 values), significance of the regression (p-values), and under- or overestimation of the mathematical correction (alignment of the data cloud to the hypothetical 1:1 fit line), the most suitable mathematical correction was selected and applied to all consumers to produce final $\delta^{13}\text{C}'$ values.

Once the final consumer $\delta^{13}\text{C}'$ data matrix was produced, $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ biplots were created to assess trophic structure at all sites. It should be noted that our across-site comparisons are biased by the fact that not all taxa were exhaustively collected at all

sites. However, this also represents the real trend that not all taxa occurred at all sites, reflecting different species diversity across sites. We are confident that we did collect the most common macroalgal and invertebrate taxa at each site, with a focus on common taxa at each site and across sites. Therefore, conclusions about trophic structure (food web length and niche width) will need to be considered with care, but these metrics will still provide valuable and representative information. To analyze food web length, we used the sponge *Dendrilla antarctica*, collected at 13 of the 15 sites, as the baseline for TL calculations, given that a primary consumer is considered to provide a more stable, time-integrated food web baseline (Vander Zanden & Rasmussen 1999, Post 2002, Iken et al. 2010). In addition, the variety and uncertainty of primary producers (a large number of macroalgae overall, and POM values from this late in the year are likely dominated by heterotrophic microorganisms) make it difficult to assign a primary producer baseline for TL calculations. At the 2 sites (I and K) where *D. antarctica* was not collected, TL was not calculated. We used an average trophic enrichment factor (TEF) of 3.4‰ for $\delta^{15}\text{N}$ to assess TLs (Vander Zanden & Rasmussen 2001, Post 2002):

$$\text{TL}_{\text{Consumer}} = ([\delta^{15}\text{N}_{\text{Consumer}} - \delta^{15}\text{N}_{D. \text{antarctica}}] / 3.4) + 2 \quad (6)$$

We are aware that TEFs are unlikely to be constant across TLs within a food web (Hussey et al. 2014), but for comparative purposes within our study, we propose it to be useful to use a fixed TEF in this pragmatic manner. Food web length was then calculated as the maximum TL per site (see Eq. 6). Trophic niche width was calculated as the convex hull of consumer stable carbon and nitrogen isotope values at each site, where the hull encompasses the smallest area in isotope space encompassed by the organisms at a site (Layman et al. 2007, Cucherousset & Villéger 2015). Niche width (convex hull area) across visually assessed site groupings was compared using 1-way ANOVA with Tukey HSD pairwise comparisons.

Relationships of benthic invertebrate feeding type stable isotope values, as well as those of individual macroalgae and invertebrate taxa (only those that occurred at 3 or more sites were included), were established with mean annual sea ice concentrations and macroalgal cover across stations. Invertebrate taxa were assigned feeding types based on literature information or our own ecological knowledge (see Table 3). Assigned feeding types included suspension feeders, indicating the capture of detrital or small phytoplankton particles from suspension through fil-

tration processes (e.g. sponges) or use of tentacles (e.g. bryozoans, octocorals); grazers that consume macroalgae by scraping the thallus (e.g. gastropods) or biting off thallus pieces (e.g. some amphipods); detritus feeders that gather detrital particles from the seafloor (e.g. with the use of sticky tentacles in terebellid polychaetes); omnivores that opportunistically consume a wide variety of diets, and predator/scavengers that actively hunt for live prey or consume carrion. It should be noted that many consumers in polar regions exhibit a certain level of omnivory, and feeding type classifications should not be seen rigorously but still provide a useful framework for testing relationships with environmental conditions over large spatial scales (e.g. Bridier et al. 2021, Zinkann et al. 2021).

For mean annual sea ice concentrations, weekly NIC charts were gridded at 1 km resolution and time series from the nearest grid cell to each sampling site were extracted from a 5 yr interval (2014–2019) at each site (Table 1). This time frame was chosen to reflect recent sea ice conditions including interannual variation (Eayrs et al. 2019), and considering the longevity of the mostly perennial macroalgae (Wiencke & Clayton 2002) and benthic invertebrates (Arntz et al. 1992). Macroalgal cover was calculated from quantitative assessments of SCUBA transects between 40 and 5 m depth at each site, as described in detail by Amsler et al. (2023). Briefly, the seafloor across this depth range was video-recorded along 3 replicate vertical transects about 100 m apart at each site. Every 5 m depth interval on each of the replicate transects, a 5 m long horizontal section along the isobath was added for increased coverage. Two laser pointers on the video camera allowed for size scaling of the recorded area, and hand-collections of macroalgae along the video transects were used for species verifications. Non-overlapping still images were produced from the video recordings, and randomly selected images from the vertical and horizontal transect components were used for analysis. Fifty randomly assigned points along a grid overlaid onto each image were analyzed for macroalgal species, invertebrate species, and substrate type. Points indicating macroalgal cover were used to quantify overall macroalgal cover for each image and extrapolated to the site level.

2.4. Statistical analyses

A mixed effects model ('lme4' package in R, Bates et al. 2015) with a random site effect was used for

these analyses between isotope data and NIC sea ice cover or macroalgal cover to account for any site-to-site variability that cannot be explained by ice cover or macroalgal cover:

$$Y_{si} = \alpha + a_s + \beta \times \text{factor}_s + e_{si} \quad (7)$$

where Y_{si} is the isotope value for replicate i at site s , α is the overall intercept, a_s is a site-specific intercept (a random effect to account for between-site variability), β is the (linear) coefficient for the ice effect, factor_s is the mean ice concentration or macroalgal cover at site s , and e_{si} is the residual for replicate i at site s (i.e. within-site variability). The model with mean macroalgal cover was not run for Site X, as macroalgal cover was not determined for that site.

Mixed effects model analyses were performed in the R language environment (v 4.2.1). Significance for all analyses was set at $\alpha = 0.05$.

3. RESULTS

3.1. Lipid bias of $\delta^{13}\text{C}$ values in Antarctic invertebrates

The average C:N value of benthic invertebrates was >3.5 in 30 out of 33 taxa, warranting lipid-correction of the $\delta^{13}\text{C}$ values (Table S2). Comparison of chemically extracted to mathematical lipid correction showed that all equations performed well, but were highly variable with regards to the specific taxon investigated. We decided to use the correction according to Alexander et al. (1996) consistently for all taxa, based on the higher p-values and R^2 values with little bias of over- or underpredicting $\delta^{13}\text{C}'$ values among the 3 approaches for most species (Table S3). Consequently, mathematically corrected $\delta^{13}\text{C}'$ values according to Alexander et al. (1996) were used in all subsequent analyses.

3.2. Carbon and nitrogen isotope ranges of primary producers and invertebrates

Within the macroalgae, $\delta^{13}\text{C}$ values ranged from -36.1‰ in *Phyllophora antarctica* to -14.5‰ in *Iridaea cordata*, and for $\delta^{15}\text{N}$ from -1.0‰ in *P. antarctica* to 5.8‰ in *Desmarestia menziesii*, when compared across all sites (Table S1). Within the red algae, 2 groups could be distinguished based on their $\delta^{13}\text{C}$ values. The first was a group highly depleted in

^{13}C (*P. antarctica*, *Myriogramme mangini*, *Plocamium* sp., and *Hymenocladopsis* sp.), with $\delta^{13}\text{C}$ values ranging from -36.1 to -32.1 ‰ across all sites (Fig. 2, Table 2, Table S1). The second group was more enriched in ^{13}C (*Iridaea cordata*, *Trematocarpus antarcticus*, *Callophyllis atosanguinea*) and ranged from -28.1 to -14.6 ‰ (although most values were between -24 and -20 ‰) across all sites, with values typically slightly higher than most brown algae (Fig. 2, Table 2, Table S1). Brown algae (*Desmarestia* spp., *Himantothallus grandifolius*) fell in between these 2 red algal groups, ranging from -34.1 to -21.4 ‰, with *Desmarestia anceps* having the lowest $\delta^{13}\text{C}$ values within that group and on occasion overlapping with the $\delta^{13}\text{C}$ values of the highly depleted red algal group (Fig. 2, Table 2, Table S1). Benthic diatoms were collected at 4 sites and had $\delta^{13}\text{C}$ values between -24.2 and -21.4 ‰, overlapping with many of the macroalgae. POM $\delta^{13}\text{C}$ values across the 13 sites where this sample type was collected covered a narrow range of $\delta^{13}\text{C}$ values, overlapping with many brown algae and only slightly lower than benthic diatoms (Fig. 2, Table S1). In terms of $\delta^{15}\text{N}$ values, groupings among the primary producers were less distinct. The above-mentioned, highly ^{13}C -depleted red algal group had $\delta^{15}\text{N}$ values between -1.0 and 5.7 ‰, while the other red algal group had $\delta^{15}\text{N}$ values between 2.5 and 5.8 ‰. Brown algal $\delta^{15}\text{N}$ values also were within a similar range, between -0.4 and 5.8 ‰. Benthic diatom $\delta^{15}\text{N}$ values were on the lower end of this spectrum (-0.1 to 2.3 ‰), but these values were derived from only 4 sites. POM $\delta^{15}\text{N}$ values were relatively low compared to other primary producers, but also overlapped largely with other algal

groups and ranged from -0.3 to 3.3 ‰ (Fig. 2, Table S1). Combined in isotope space, some algal groupings could be identified, although with much overlap (Fig. 2).

Invertebrate $\delta^{13}\text{C}'$ values ranged from -32.2 to -11.2 ‰ in the sponge *D. antarctica* and the sea star *Odontaster validus*, respectively, thus overlapping well with potential primary producer sources in their lower stable carbon isotope range, but extended in most cases well beyond food sources in the more ^{13}C -enriched values (Table S2). As expected, lower TL consumers such as suspension feeders tended to have lower $\delta^{13}\text{C}'$ values, while predators/scavengers tended to have higher $\delta^{13}\text{C}'$ values (Table 3). $\delta^{15}\text{N}$ values of invertebrate consumers ranged from 2.5 ‰ in the sponge *D. antarctica* to 15.3 ‰ in the sea star *Labidiaster annulatus*, again reflecting an expected trend across feeding types (Table 3).

3.3. Relationships of primary producer and consumer stable isotope composition with sea ice cover

Only 1 macroalgal species exhibited a significant relationship between stable isotope values and annual average NIC sea ice cover. Contrary to expectation, only the $\delta^{15}\text{N}$ values of the red alga *I. cordata* and none of the $\delta^{13}\text{C}$ values of any macroalgal species increased significantly with increasing sea ice cover (Table S4). Several of the invertebrate $\delta^{13}\text{C}'$ and $\delta^{15}\text{N}$ values were significantly related to annual average NIC sea ice cover, either positively or negatively, and typically for taxa occupying lower TLs (Table S5).

Table 2. Average stable nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotope values and C:N ratios of the most common primary producers. Averages are given for the number of sites at which a taxon was sampled

Algal taxon	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	C:N	n sites
Microalgae				
Benthic diatoms	1.02	-22.57	6.58	4
Particulate organic matter (POM)	1.32	-25.43	5.65	13
Phaeophyceae				
<i>Desmarestia anceps</i>	0.13	-33.30	12.65	2
<i>Desmarestia menziesii</i>	3.89	-25.90	13.90	12
<i>Desmarestia antarctica</i>	2.60	-25.60	12.61	3
<i>Himantothallus grandifolius</i>	1.61	-24.88	18.58	9
Rhodophyta				
<i>Callophyllis atosanguinea</i>	4.15	-21.19	6.41	3
<i>Hymenocladopsis</i> sp.	1.89	-33.39	6.59	6
<i>Iridaea cordata</i>	4.63	-21.50	12.94	11
<i>Myriogramme mangini</i>	3.32	-34.23	7.93	8
<i>Phyllophora antarctica</i>	1.33	-34.51	6.96	5
<i>Plocamium cartilagineum</i>	3.05	-33.52	7.85	9
<i>Sarcopeltis antarctica</i>	2.32	-24.47	14.68	3
<i>Trematocarpus antarcticus</i>	3.82	-23.12	6.51	7

Table 3. Average stable nitrogen ($\delta^{15}\text{N}$) and mathematically corrected carbon ($\delta^{13}\text{C}'$) isotope values and C:N ratios of the most common invertebrate taxa. Averages are given for the number of sites at which a taxon was sampled. References for invertebrate feeding type classification are provided

Invertebrate taxon	Feeding type	$\delta^{15}\text{N}$	$\delta^{13}\text{C}'$	C:N	n sites	Reference
Porifera						
<i>Dendrilla antarctica</i>	Suspension feeder	4.32	-23.51	4.31	13	Leiva et al. (2019)
Cnidaria						
<i>Isotealia antarctica</i> ^a	Predator/scavenger	9.77	-17.77	4.32	10	Bryan et al. (1998), Amsler et al. (1999)
Octocorallia	Suspension feeder	6.70	-21.89	4.30	8	Gili et al. (2001), Orejas et al. (2003)
Bryozoa						
lobed	Suspension feeder	3.12	-24.73	3.46	3	Pratt (2008)
Mollusca						
<i>Austrodroris kerguelensis</i>	Predator/scavenger	7.25	-16.79	4.97	7	Wägele (1989)
<i>Nacella concinna</i>	Grazer	6.47	-14.64	3.88	15	Iken (1996), Choy et al. (2011), Morley et al. (2014), Suda et al. (2015)
Arthropoda						
<i>Margarella antarctica</i>	Grazer	6.94	-16.18	3.68	9	Linse et al. (2006), Schram et al. (2014)
<i>Marseniopsis mollis</i>	Predator/scavenger	8.24	-21.28	3.91	4	McClintock et al. (1994)
Polynoidae	Detritus feeder	5.67	-15.61	4.16	4	Drennan et al. (2021)
Terebellida	Detritus/scavenger	9.95	-16.80	3.16	11	Drennan et al. (2021)
	Detritus feeder	7.48	-18.71	4.08	6	Miller et al. (1992)
<i>Bovallia gigantea</i>	Predator/scavenger	8.18	-17.90	4.19	8	Bone (1972), Aumack et al. (2017)
<i>Eusinus bouvieri</i>	Predator/scavenger	7.24	-19.23	4.58	4	De Broyer et al. (2004)
<i>Gondogeneia antarctica</i>	Grazer	5.72	-17.25	5.31	10	Huang et al. (2006), Aumack et al. (2017)
<i>Metaleptamphopus pectinatus</i>	Omnivore	5.57	-21.01	7.30	5	M. O. Amsler pers. comm.
<i>Oradarea bidentata</i>	Grazer	5.76	-18.66	5.34	7	Bucolo et al. (2011), Aumack et al. (2017), Michel et al. (2020)
<i>Paradoxamine fissicauda</i>	Grazer	4.80	-27.65	4.41	7	Amsler et al. (2013), Aumack et al. (2017), Heiser et al. (2022)
<i>Paraphimedia integricauda</i>	Grazer	6.81	-20.74	5.26	4	Aumack et al. (2017)
<i>Pontogeneilla brevicornis</i>	Omnivore	4.89	-17.56	5.78	7	M. O. Amsler pers. comm.
<i>Protebbingia gracilis</i>	Omnivore	5.84	-19.53	7.62	7	Aumack et al. (2017)
<i>Glyptonotus antarcticus</i>	Predator/scavenger	10.29	-17.72	3.10	5	Dearborn (1967)
Echinodermata						
<i>Cuenotaster involutus</i>	Predator/scavenger	11.67	-14.79	4.43	5	Thomassin (1976), Presler (1986), McClintock (1994)
<i>Diplasterias brandti</i>	Predator/scavenger	8.62	-19.53	3.79	11	McClintock (1994)
<i>Glabaster antarctica</i>	Predator/scavenger	10.07	-16.11	3.98	5	McClintock (1994), Bowden et al. (2011)
<i>Labidiaster annulatus</i>	Predator/scavenger	12.72	-18.19	3.87	6	McClintock (1994)
<i>Neosmilaster georgianus</i>	Predator/scavenger	9.47	-15.58	4.21	11	McClintock (1994)
<i>Odontaster validus</i>	Omnivore	10.53	-15.89	3.97	15	Presler (1986), McClintock (1994), Zenteno-Devaud et al. (2022)
<i>Perknaster aurorae</i>	Predator/scavenger	11.10	-18.08	3.98	7	McClintock (1994)
<i>Heterocucumis cucumaris</i>	Suspension feeder	8.02	-21.76	3.72	5	Clarke & Peat (2022)
<i>Holothuroidea pink</i>	Detritus feeder	6.12	-22.07	5.07	3	Clarke & Peat (2022)
<i>Sterechinus neumayeri</i>	Omnivore	7.79	-15.93	3.94	12	McClintock (1994), Brockington et al. (2001), Jacob et al. (2003)
Chordata						
<i>Cnemidocarpa</i> sp.	Suspension feeder	5.55	-23.65	3.83	14	Tatián et al. (2008), Lesser & Slattery (2015)

^aSmall individuals of *Isotealia antarctica* can be confused with *Urticinopsis antarctica*, which also occurs along the Western Antarctic Peninsula. Since all individuals in our collection were larger, we are confident that our collections were *I. antarctica*

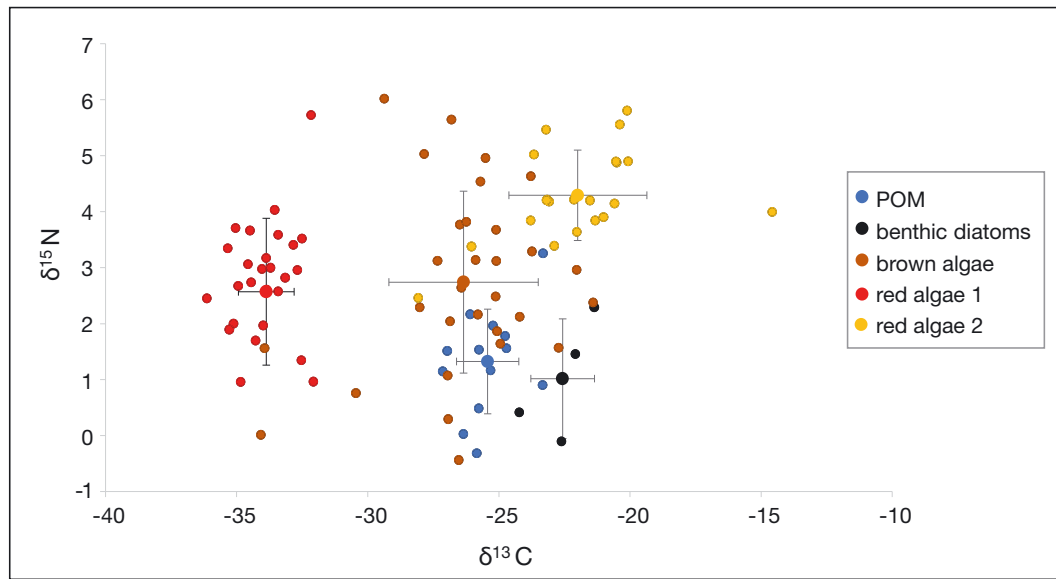


Fig. 2. Stable carbon and nitrogen isotope values of various primary producer groups across all sites. POM: particulate organic matter. Individual points are species means (from up to $n = 3$ replicates per sample) at a site, color coded here by primary producer group. Larger points ($\pm$ SD) are averages of these groupings across all sites

Of these relationships, the positive relationship of the amphipod grazer *Paradexamine fissicauda* $\delta^{13}\text{C}'$ values with sea ice cover was the strongest ($p < 0.001$), explaining approximately 92% of the variation. Explanatory power of other relationships was less than 50% (Table S5).

For a broader perspective, we also assessed relationships of sea ice cover with the $\delta^{13}\text{C}'$ and $\delta^{15}\text{N}$ values of invertebrates grouped by feeding types (Table 4, Fig. 3). Clear patterns emerged, where the $\delta^{15}\text{N}$ values of all feeding groups except for detritus feeders and omnivores were significantly and positively influenced by average annual sea ice cover. However, explanatory power was relatively low, the highest being 27% of the variability explained within the suspension feeders. Average annual sea ice cover was a significant predictor of $\delta^{13}\text{C}'$ values of all feeding types, with the highest explanatory power for suspension feeders with 24% of the variability (Table 4, Fig. 3).

3.4. Relationships of consumer stable isotope composition with macroalgal cover

We also analyzed the relationship between consumers and feeding types

and macroalgal cover, which may have a more direct association with consumers than sea ice cover. Since average annual sea ice cover and macroalgal cover are highly inversely correlated (see Amsler et al. 2023), results were similar to correlations observed with sea ice cover (Fig. 4, Table 5, Table S6). However, some of the relationships detected with sea ice cover were no longer significant with macroalgal cover. Similarly, several of the relationships of feeding types that were significantly related to sea ice cover were no longer significant when related to macroalgal cover (Table 5, Fig. 4). Only the isotope values ($\delta^{13}\text{C}'$ and $\delta^{15}\text{N}$) of suspension feeders and the $\delta^{15}\text{N}$ of predators/scavengers retained a significant relationship

Table 4. Results of a mixed effects model with a random station effect to test for the relationship between invertebrate feeding type stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) and the average annual sea ice cover from National Ice Center (NIC) ice charts at each station. Given are the parameter estimates, p-values for the slope, and the marginal R^2 values that provide the proportion of the overall variability in the response to the fixed effect, ice cover. Significant ($p < 0.05$) relationships are in **bold**

Feeding type	$\delta^{15}\text{N}$			$\delta^{13}\text{C}'$		
	Estimate	p	R^2	Estimate	p	R^2
Suspension feeders	0.06	<0.001	0.269	0.07	0.001	0.242
Grazers	0.02	<0.001	0.042	0.08	0.049	0.052
Detritus feeders	0.01	0.848	0.002	0.09	0.040	0.159
Omnivores	0.03	0.112	0.029	0.07	0.022	0.135
Predator/scavengers	0.03	0.015	0.055	0.04	0.048	0.049

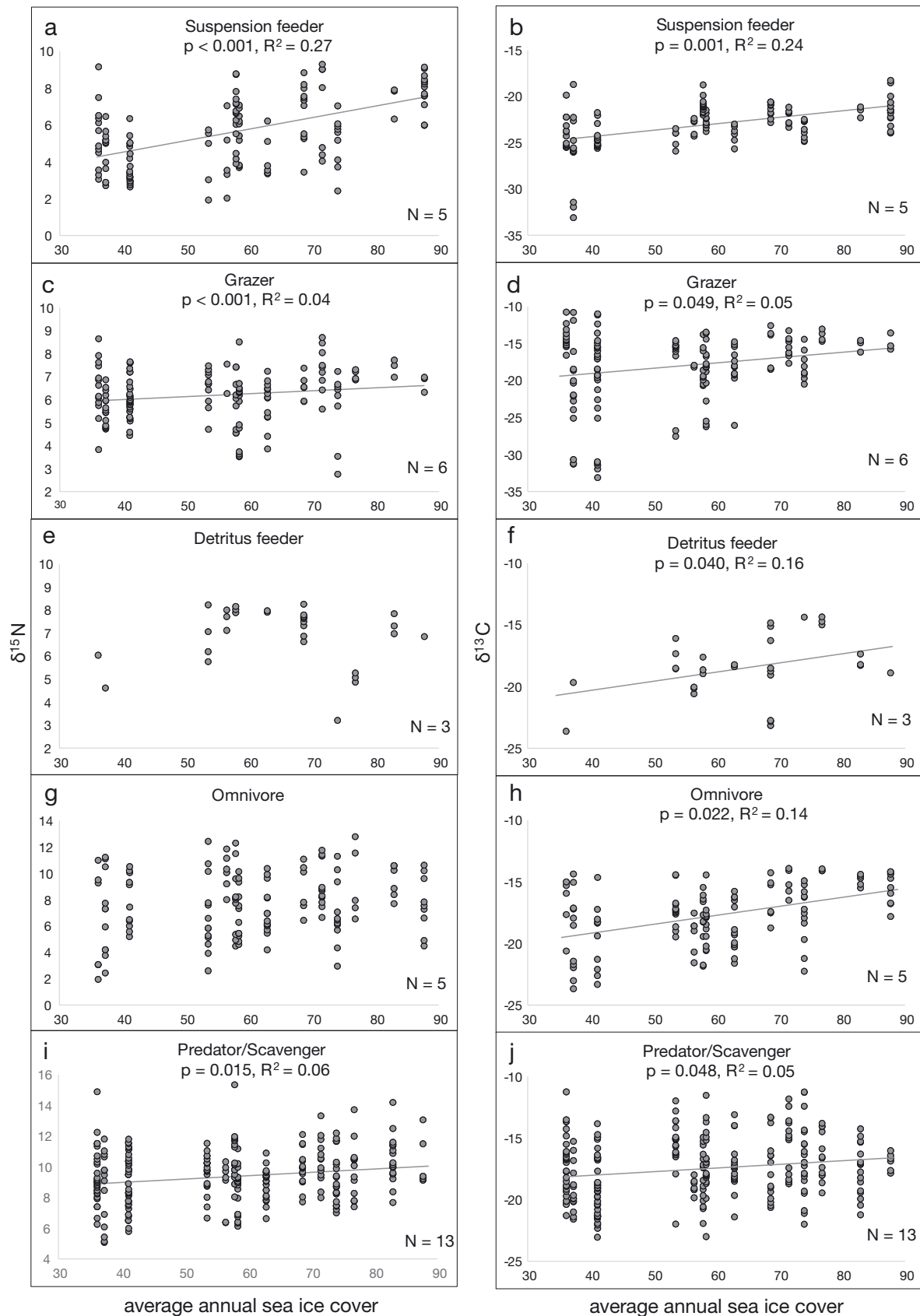


Fig. 3. Relationship between stable isotope values ($\delta^{15}\text{N}$ or $\delta^{13}\text{C}$) of invertebrate feeding types with average annual sea ice cover, based on National Ice Center data (2014–2019 average). See Table 4 for details. N: number of taxa included in a feeding type

Table 5. Results of a mixed effects model with a random station effect to test for the relationship between invertebrate feeding type stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) and the average macroalgal cover at each station. Given are the parameter estimates, p-values for the slope, and the marginal R^2 values that provide the proportion of the overall variability in the response to the fixed effect, macroalgal cover. Significant ($p < 0.05$) relationships are in **bold**

Feeding type	$\delta^{15}\text{N}$			$\delta^{13}\text{C}$		
	Estimate	p	R^2	Estimate	p	R^2
Suspension feeders	-0.03	<0.001	0.300	-0.04	<0.001	0.333
Grazers	0.00	0.309	0.017	-0.04	0.066	0.052
Detritus feeders	-0.01	0.674	0.010	-0.05	0.086	0.119
Omnivores	-0.01	0.228	0.018	-0.03	0.053	0.100
Predator/scavengers	-0.01	0.011	0.057	-0.02	0.014	0.066

with macroalgal cover. Similar as for relationships with sea ice cover, explanatory power was relatively low for those significant relationships with macroalgal cover.

3.5. Trophic structure across sites

Visually exploring the arrangement of primary producers and consumers in isotope space of the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ biplots across all sites (Fig. 5), 3 broad groups could be distinguished. The first group, at more northern sites (A–G), was characterized by large trophic niche width, mostly 4 TLs with the sponge *D. antarctica* as a baseline (Table 6), and overlap of consumer niche width at the lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value range with primary producers (Fig. 5). One of those consumers with particularly low $\delta^{13}\text{C}$ values (typically $< -26\text{‰}$) was the amphipod grazer *P. fissicauda*, suggesting a tight trophic connection to especially the highly ^{13}C -depleted red algal group (see arthropod with low $\delta^{13}\text{C}$ values in Fig. 5). Other consumers typically overlapping much with the primary producers at this first site group were suspension feeders, specifically the sponge *D. antarctica*, bryozoans, and the ascidian *Cnemidocarpa* sp. (Fig. 5). At sites where they occurred, the suspension feeders Octocorallia and the predator/scavenger sea star *Diplasterias brucei* had relatively low $\delta^{13}\text{C}$ values, but with typically higher $\delta^{15}\text{N}$ values than the grazers or other suspension feeders (Table 3, Fig. 5). An outlier from this group was Site A, where we calculated less than 4 TLs (3.7), but we contend that this was driven by an unusually high $\delta^{15}\text{N}$ value for *D. antarctica* at that site (5.57‰), while at other sites within this group, including spatially very close groups, the $\delta^{15}\text{N}$ value was between 2.47 and 3.43‰. With a TEF of 3.4‰, this average difference accounts

for about two-thirds of a TL. In addition, the $\delta^{15}\text{N}$ values of *D. antarctica* and the lobed bryozoan at other sites where they co-occurred (Sites B and C) were very similar (see Table S2). The $\delta^{15}\text{N}$ value of the bryozoan at Site A was 3.12‰, much closer to the typical $\delta^{15}\text{N}$ value of *D. antarctica*. Hence, the low calculated number of TLs at Site A may not reflect the actual food web structure well at that site. Using the average $\delta^{15}\text{N}$ value of *D. antarctica* for this site group excluding Site A (3.13‰), food web length at Site A would be 4.4. At the upper end of the

trophic spectrum (around TL 4 and higher) we typically found a variety of predator/scavengers, specifically sea stars (*Neosmilaster georgianus*, *Odontaster validus*, *Perknaster aurora*, *Labidiaster annulatus*, *Cuenotaster involutus*), polynoid worms, the anemone *Isotealia antarctica*, and the amphipod *Bovalia gigantea* (Fig. 5, Table S2).

A second site group visually identified based on the trophic structure metrics were Sites H through L (Fig. 5), occupying the mid-latitudinal and intermediate sea ice cover range of our study region. The food webs at these sites still contained about 4 TLs (Table 6), but with much less overlap with the isotope values of primary producers at the lower invertebrate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value spectrum. This was reflected in a significantly smaller trophic niche width than in the first site group (overall ANOVA, $F_{2,12} = 12.53$, $p = 0.001$, HSD pairwise comparison $p = 0.001$). For the most part, these sites contained slightly fewer primary producers than sites in Group 1, in one case likely due to local effects of recent ice scouring (Site K, see Amsler et al. 2023), but also reflecting an actual decline in macroalgal species richness (Table 1). Even at sites that still contained relatively many macroalgal species (Sites H–J), consumers rarely overlapped with those in isotope space. This trend was mostly related to the lack of grazing species with low $\delta^{13}\text{C}$ values (especially many amphipods) at these sites. It is unlikely that these taxa were simply missed during our collections as similarly extensive airlift sampling was conducted at these sites as at other sites. Even at Site J, where a number of grazing amphipods were collected (Table S2), the overlap in $\delta^{13}\text{C}$ values with those of macroalgae at that site was limited (Fig. 5). The upper TLs at these sites were still occupied by predators/scavengers, such as the sea stars, anemones, polynoids, etc., as for the previous site group.

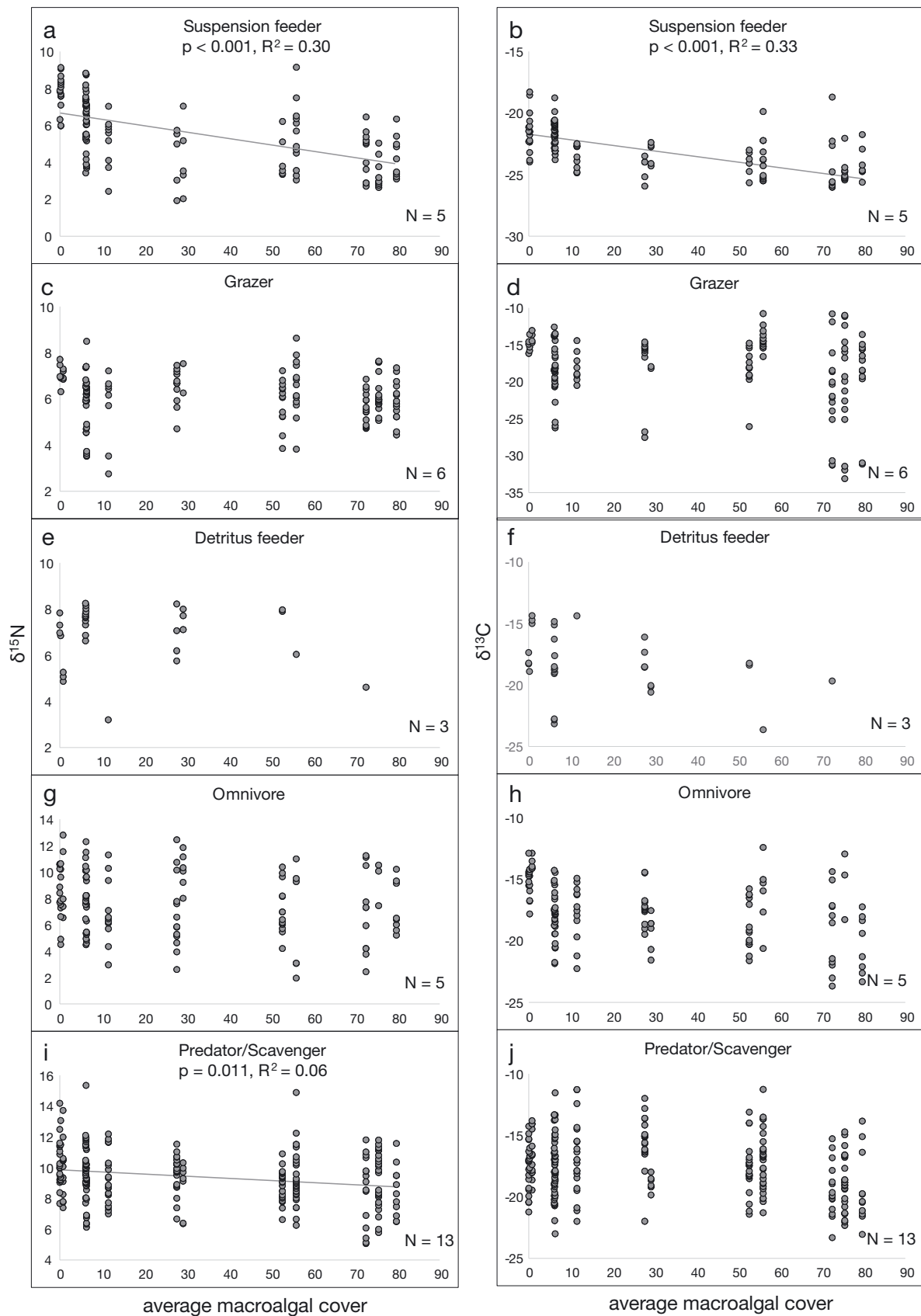


Fig. 4. Relationship between stable isotope values ($\delta^{15}\text{N}$ or $\delta^{13}\text{C}$) of invertebrate feeding types with average macroalgal cover at a site. See Table 5 for details. N: number of taxa included in a feeding type

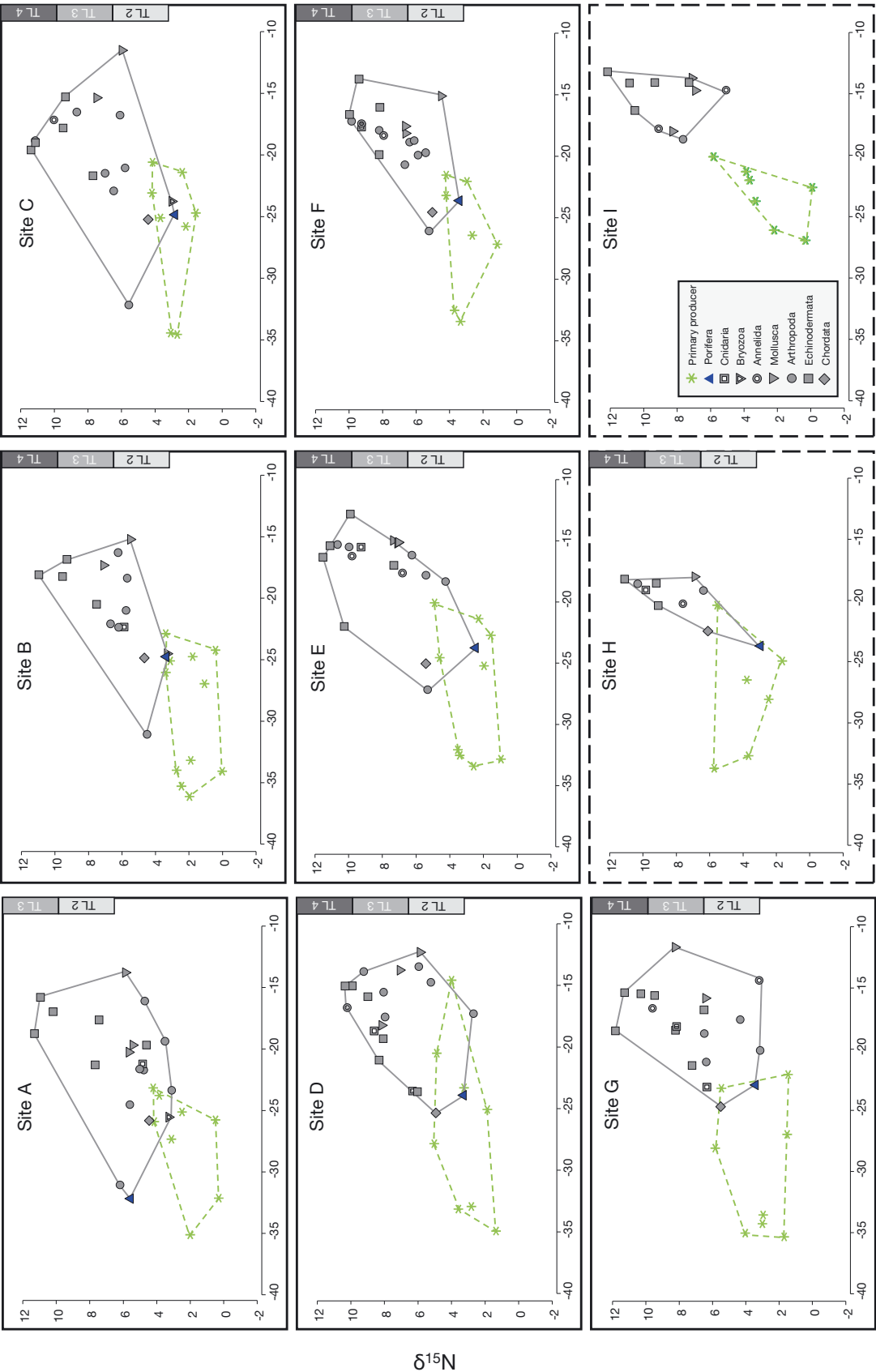


Fig. 5. $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplots for primary producers (green stars) and common invertebrate consumers (gray markers) at each site. Invertebrates are coded by phylum. Stable isotope values of Porifera (the sponge *Dendrilla antarctica*), which was used as the primary consumer baseline to calculate trophic levels (TLs), are indicated with a blue triangle. Calculated TLs based on a 3.4‰ trophic enrichment factor are indicated by the bars on the right of each station plot. Invertebrate niche width is indicated by the gray convex hull outline. Primary producers are outlined by a green, dashed convex hull, although they are not part of the trophic niche calculation. Station plot outline indicates visually identified groupings of similar trophic structure: Group 1, solid frame (Sites A–G); Group 2, dashed frame (Sites H–I); Group 3, dotted frame (Sites X, M, and N)

(Fig. 5 continued on next page)

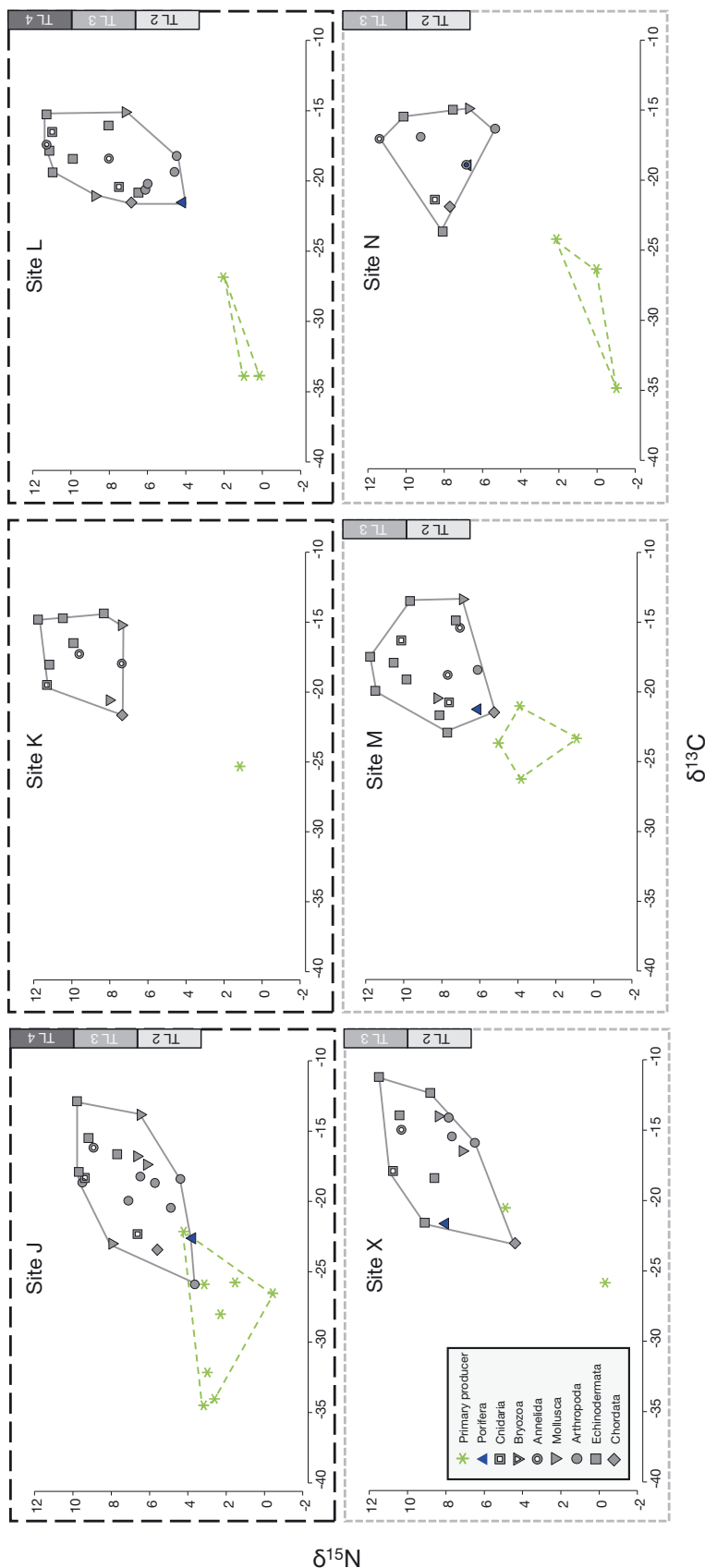


Fig. 5. (continued)

The third, visually identified site group comprised the more southern Sites X, M, and N (Fig. 5). Only a few primary producers occurred at these sites, which were isotopically well separated from the consumers. The food web at these sites comprised less than 4 TLs (Table 6), driven by higher $\delta^{15}\text{N}$ values of primary consumers such as *D. antarctica*, *Cnemidocarpa* sp., and also grazing amphipods such as *Gondogeneia antarctica*, where they occurred. Trophic niche width again was lower than in site Group 1 (Tukey HSD $p = 0.014$) but was not different from niche width in site Group 2 (Tukey HSD $p = 0.845$). The higher TLs were again occupied by the same taxa as in previous site groups, but classified around TL 3 or slightly above, based on the shifted *D. antarctica* baseline.

4. DISCUSSION

Seasonal sea ice cover is a major driver of the abundance of many, if not most, taxa and biological processes in the Southern Ocean, including those along the coast of the WAP (Constable et al. 2014). Along the WAP, sea ice cover also significantly influences the abundance of macroalgal primary producers (Amsler et al. 2023), with potential impacts on the coastal benthic food web. Here, we found that overall food web structure changed along a gradient of sea ice cover from around Anvers Island to the Marguerite Bay region. Despite much lower macroalgal diversity at sites with higher average sea ice cover, the contraction into a shorter food web was associated more with a shift in primary consumers to higher TLs and less with a shift of the macroalgal and POM primary producers at the base of the food web. These shifts suggest that the larger diversity of primary producer sources at sites with less annual sea ice cover support a more diverse food web with more specialized consumers, while at sites with higher average annual sea ice

Table 6. Food web length (maximum trophic level, TL) and trophic niche width (isotope convex hull of consumers) of food webs at sites along the Western Antarctic Peninsula. Visually assessed site groupings (see Fig. 5) are separated by dashed lines; nd: not determined

Site	Max. TL	Niche width (‰ ²)
A	3.7	89.5
B	4.2	58.8
C	4.5	91.4
D	4.8	76.5
E	4.7	70.4
F	3.9	46.6
G	4.5	75.2
H	4.4	17.1
I	nd	31.8
J	3.8	49.0
K	nd	24.5
L	5.3	45.2
X	3.4	47.6
M	3.7	42.4
N	3.3	28.1

cover, consumers derive energy from a smaller, more homogeneous organic matter pool that has likely undergone increased heterotrophic (bacterial) processing steps, resulting in a more homogeneous consumer web.

4.1. Lack of shifts in food primary producer baselines across the sea ice gradient

Macroalgal biogeochemical, biochemical, and pigment compositions are known to respond to a seasonally variable light regime in polar oceans (Wiencke & Fischer 1990, Aguilera et al. 2002), which, under natural conditions in polar systems, is strongly influenced by annual sea ice cover (Odate et al. 2004, Singh et al. 2022). We expected to see this influence of lower annual light availability reflected in the carbon stable isotope values of macroalgae along the sea ice cover gradient sampled in this study (following Wiencke & Fischer 1990). Instead, there was no significant change in $\delta^{13}\text{C}$ of any of the macroalgal species across sites, indicating similar carbon fractionation across environmental conditions. This is similar to findings for various macroalgal species analyzed for photosynthetic performance and related parameters, including $\delta^{13}\text{C}$ values, under high and low light conditions in East Antarctica (Runcie & Riddle 2006). This includes consistent patterns of stable isotope values within red algal groups based on carbon-concentration mechanisms, especially the lack of

pyrenoids and instead diffusive carbon uptake in some red algal species that are highly depleted in ^{13}C (Raven et al. 2002), indicating that these are robust groupings to serve as primary producer biomarker inputs into food web models.

Our finding that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of all primary producers were largely similar across the latitudinal and sea ice gradients suggested that there was little shift in the primary producer baseline of the food web. This is opposite to findings of a similar study of macroalgal stable isotope values in the large brown algae along a latitudinal gradient from the northern part of the WAP to Rothera, which was then linked to a shift in food web baseline (Cardona et al. 2021). Possible explanations of the differences in the macroalgal patterns of that study compared to ours may be related to the timing of sampling. Cardona et al. (2021) sampled in February, representing late summer season, while our April–May sampling is reflective of autumn conditions. These seasonal differences translate into differences in light intensity, and consequently photosynthetic rates and growth (Gomez & Wiencke 1997), which could influence stable isotope composition. Growth of Antarctic macroalgae is higher during periods of increased light intensity, i.e. in summer, resulting in higher (more ^{13}C -enriched) carbon isotope values (Wiencke & Fischer 1990). Likely, this is caused by high carbon uptake rates during high rates of photosynthesis and growth during which there is local (in the boundary layer along the thallus) drawdown of the preferred ^{12}C substrate and less discrimination against the ^{13}C substrate (Raven et al. 2002). Therefore, stable isotope patterns in macroalgae during the peak growth season in summer (Cardona et al. 2021) could be different from patterns observed here during the autumn season, indicating that food web structure responses to sea ice cover may be a seasonally dynamic feature.

4.2. Consumer patterns across the sea ice gradient

The relationship between consumer $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values and sea ice cover was positive, where one existed. Conversely, those same relationships were negative when related to macroalgal cover based on the negative relationship between sea ice cover and macroalgal cover (Amsler et al. 2023). This positive relationship between consumers and average annual sea ice cover occurred with the $\delta^{13}\text{C}$ values, indicating a shift in the food source, while the change in $\delta^{15}\text{N}$ values indicated a shift in trophic position. These relationships with sea ice cover were particu-

larly strong in suspension feeders, with examples being the sponge *Dendrilla antarctica*, octocorals, and the ascidian *Cnemidocarpa* sp. While individual consumer species reflected these trends to various degrees, the feeding type groups across these gradients supported these patterns more strongly, likely because of the higher sample size and buffering of variability in individual species. While we did not find sea ice cover-related changes in the isotope values of most macroalgae, the actual local detrital, benthic sources from macroalgal debris that are consumed by suspension feeders may exhibit differences in stable isotope values, which then translate into consumers. These isotope changes in the detrital pool are typically driven by additional steps in microbial processing (i.e. additional trophic steps) that will increase the $\delta^{15}\text{N}$ values of the detrital pool (e.g. Iken et al. 2010, Leclerc et al. 2013, Lowe et al. 2014, Bell et al. 2016). These results match those found in the Ross Sea, where invertebrate consumers, especially lower TL suspension and detrital feeders, had lower $\delta^{15}\text{N}$ values in regions of longer open-water periods, reflecting more phytoplankton consumption, while the same taxa in locations of longer ice cover were more dependent on isotopically enriched detrital sources (Norkko et al. 2007).

One producer source that is typically associated with higher $\delta^{13}\text{C}$ values is sea ice algae, which we were unable to collect during our project. However, in other regions of the Southern Ocean (Ross Sea), sea ice algae significantly influenced the diet spectrum and stable isotope composition of common invertebrate consumers, as well as the entire food web organization (Rossi et al. 2019, Caputi et al. 2020). Accordingly, the longer sea ice cover in our more southern study region could have greater input of ^{13}C -enriched sea ice algae into the benthic coastal food web (Wing et al. 2018), adding a possible explanation for the increases in isotope values of several feeding types with longer sea ice cover.

4.3. Food web structure across the sea ice cover gradient

There were few isotopic changes at the base of the food webs across sites, only a decrease in the diversity of primary producer sources across sites with increasing sea ice cover. This sequential decrease in macroalgal species, in particular, may have had more influence on food web structure than any isotopic shift in the primary producer baseline. For example, at more northern sites with shorter sea ice cover and

larger macroalgal cover and diversity (first site group A–G in Fig. 5), we found several consumers that seemed tightly linked to some of the macroalgal sources. For example, the grazing amphipod *Paradexamine fissicauda* had extremely low $\delta^{13}\text{C}$ values, closely related to the low $\delta^{13}\text{C}$ values of the red algal Group 1 (see Fig. 2, also see Aumack et al. 2017). This amphipod species is known to consume chemically defended macroalgal species such as *Plocamium* sp. (Amsler et al. 2013, Heiser et al. 2020), which had consistently low $\delta^{13}\text{C}$ values of around -33.5‰ in our study. Once this source species started to disappear, the amphipod was also not commonly found. This is one example of how a higher diversity of sources can support a higher diversity of finely-tuned, specialized feeders. It also may suggest that specialist species like this amphipod are less competitive compared with other grazers once their specific food source disappeared. Without the benefit of being able to consume otherwise chemically defended algal species, they are unlikely to find a niche against more generalist grazing amphipods like *Gondogeneia antarctica* (Huang et al. 2006, Ahn et al. 2021).

Overall food web structure changed with increasing average annual sea ice cover, where consumers grouped closer together at sites with higher ice cover, as indicated by a decrease in food web length and trophic niche space. This pattern supports niche theory, whereby greater resource availability increases trophic niche width, as has been previously found for benthic consumers in Antarctica when examining temporal changes in resource availability (Calizza et al. 2018) or spatial patterns across small spatial scales (Le Bourg et al. 2021). Estimations of food web length are sensitive to both horizontal (source) and vertical (consumer) diversity dimensions of the assemblage (Vander Zanden & Fetzer 2007, Sokołowski et al. 2012, Wang & Brose 2018). Reduced resource availability with the much lower number of macroalgal species and coverage as seen at more ice-covered sites likely led to niche constriction and greater dietary consumer overlap. The most obvious example of this contraction in the consumer web is the sponge, *D. antarctica*. At sites with the highest sea ice cover (third site group comprising X, M, N; see Fig. 5), *D. antarctica* grouped much closer with other taxa that are considered top-level predatory invertebrates, such as several of the sea star species. This homogenization of the food web speaks to the trophic plasticity of many these coastal consumers, which seem to be able to adjust to shifts in primary producer or organic matter supply. This

matches well with earlier characterizations of many Antarctic benthic invertebrate species as opportunistic omnivores (e.g. McClintock 1994, Gili et al. 2001, Michel et al. 2016, 2019, Le Bourg et al. 2021), allowing them to be successful in a highly dynamic Antarctic coastal environment. This plasticity could be an advantageous pre-adaptation of those species to be successful in highly variable environmental conditions across large spatial scales, such as variable sea ice cover and macroalgal availability.

4.4. Conclusion

In summary, we found that the shallow-water benthic food web along the WAP showed signs of linking of multiple trophic pathways that are typically associated with more stable food webs (Huxel et al. 2002, Rooney & McCann 2012), even if these patterns could not unequivocally be related to a fast (phytoplankton-based) and slow (macroalgal-based) energy pathway, as originally assumed. Instead, several macroalgal-based pathways, based on distinct macroalgal groupings characterized by their biogeochemical signatures, provided a broad primary producer base of the food web that led to selective resource use by the consumers and a longer food web in regions of low annual sea ice cover. While the macroalgal taxa within these groupings do not differ as much in size and biomass turnover as a macroalga does from a phytoplankton cell, Antarctic macroalgal species have specific adaptations in photosynthesis, growth, and carbon storage to the highly seasonal dynamics of the coastal Antarctic system (Wiencke et al. 2007). This provides an ecological basis for horizontal (source) diversification at the base of the food web (Layman et al. 2007). The observed changes in overall food web structure in relation to the annual sea ice cover suggest that coastal communities in the more sea-ice covered study region may acquire longer food web lengths, wider consumer trophic niches, and also become more stable, as sea ice cover decreases due to global warming (Turner et al. 2013), which inevitably will influence the availability of primary producers and other food sources (Zenteno-Devaud et al. 2022). In contrast, the more homogeneous systems dominated by generalists currently encountered in regions of higher sea ice cover are less efficient in energy transfer and typically lower in diversity (Clavel et al. 2011), which can also be interpreted as less stable systems with lower adaptive capacity to disturbance.

Data availability. Data associated with this manuscript are stored at the USAP-DC under <https://doi.org/10.15784/601653>, linked to project <https://www.usap-dc.org/view/project/p0010104>

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