



Trophic stability and change across a sea ice cover gradient on the western Antarctic Peninsula

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ABSTRACT: The western Antarctic Peninsula (AP) is experiencing significant changes to sea ice cover, altering the macroalgal cover and potentially affecting the foundation of benthic food webs. We used fatty acid signatures as dietary and physiological trophic biomarkers to test the hypothesis that a gradient of 36–88% mean annual ice cover would affect the trophic ecology of fleshy macroalgae and diverse benthic invertebrate consumers along the western AP. We used SCUBA to collect organisms from benthic rocky nearshore habitats, 5–35 m depth, at 15 study sites during April–May of 2019. There were no consistent ecosystem-scale differences in the nutritionally important polyunsaturated fatty acids or other univariate fatty acid summary categories in either the seaweeds or invertebrates across the ice gradient, but we did find site-level differences in the multivariate fatty acid signatures of all seaweeds and invertebrates. Ice cover was a significant driver of the fatty acid signatures of 5 invertebrates, including 3 sessile (an anemone, a sponge, and a tunicate) and 2 mobile consumers (a sea star and a sea urchin). The multivariate fatty acid signatures of 2 other sea stars and a limpet were not affected by the ice gradient. These results indicate that the trophic ecology and resource assimilation of sessile consumers that are more connected to the macroalgal-derived food web will be more sensitive than mobile consumers to impending changes to annual ice and macroalgal cover along the western AP.

KEY WORDS: Sea ice cover · Western Antarctic Peninsula · Antarctic ecology · Fatty acid signatures · Trophic ecology · Climate change · Benthic ecosystem

1. INTRODUCTION

The manifestation of climate change is not geographically uniform; as global average temperatures continue to rise (IPCC 2022), certain areas, such as polar ecosystems, are experiencing more extreme warming rates and are particularly sensitive to climate change (Morley et al. 2019, Post et al. 2019). The

Antarctic Peninsula (AP) is one of the fastest-warming regions in the southern hemisphere (Smith et al. 1999, Bromwich et al. 2013, Siebert et al. 2019), resulting in reduced persistence and extent of ice cover, particularly in the western AP (Henley et al. 2019, IPCC. 2022). Our understanding of the importance and dynamics of sea ice-associated productivity in the Southern Ocean is largely focused on connections to

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pelagic food webs associated with primary production from phytoplankton, ice-associated microbial communities, and secondary production by zooplankton (Arrigo & Thomas 2004, Constable et al. 2014, Wing et al. 2018). However, benthic ecosystems rely on productivity from phytoplankton, microbes, benthic microalgae, and benthic seaweeds in rocky nearshore Antarctic communities (Dayton et al. 1986, Iken et al. 1997, Dunton 2001, Marina et al. 2018, Alurralde et al. 2020). The implications of warming in this region has been extensively studied for production by phytoplankton and microalgae (Moline et al. 2004, Moreau et al. 2015, Mendes et al. 2023), but less is known about the consequences to macroalgae (commonly referred to as seaweeds) as a basal resource for coastal food webs.

Climate change and warming are typically framed in terms of negative effects on ecosystem function. However, the response of ecosystems to extreme environmental changes is complex, and there will be winners and losers as conditions change (McClintock et al. 2008, Clucas et al. 2014). In benthic marine habitats of the western AP, ice cover and irradiance reaching the benthos are 2 of the most important environmental drivers affecting seaweeds, as nutrients, which are another typically limiting resource in many parts of the world, are usually not limiting or are highly variable in this system (Wiencke et al. 2007, Zacher et al. 2009). Seaweeds and basal consumers are poised to benefit from reduction in ice cover along the western AP due to an increase in available open space and light as a result of longer ice-free seasons (Constable et al. 2014). The consequences of declines in ice cover are complex and may not directly benefit primary producers; for example, both increased ice scour (Smale 2007, Barnes 2017) and the associated turbidity increase in the case of glacial meltwater may actually curtail macroalgal productivity along the western AP (Jerosch et al. 2019). Moreover, in other Antarctic sea ice gradient systems, benthic invertebrate food webs incorporate more organic matter derived from ice-associated phytoplankton and microbial producers in areas with more persistent ice (Wing et al. 2018).

Seaweeds are common foundation species in the nearshore rocky benthos of the western AP (Neushul 1965, Wiencke & Amsler 2012, Momo et al. 2020, Oliveira et al. 2020), where they contribute both directly and indirectly to coastal food webs (Iken 1999, Aumack et al. 2017). There are well-known gradients in macroalgal abundance in Antarctica due to differing physical conditions in constrained areas (Miller & Pearse 1991, Amsler et al. 1995, Klöser et al. 1996,

Wiencke & Amsler 2012), and a strong negative north to south gradient in the abundance of seaweeds at larger geographic scales (Moe & DeLaca 1976, Mystikou et al. 2014, Amsler et al. 2023, 2024). This biogeographical gradient in algal abundance is strongly correlated to sea ice cover (Amsler et al. 2023). As ice cover and associated primary production by seaweeds and phytoplankton in high latitude systems change (Ducklow et al. 2013), there will likely be cascading effects on the food web structure of the AP (McClintock et al. 2008, Iken et al. 2023).

The invertebrates of the nearshore rocky littoral habitats of the AP are connected through the food web to the basal production in the system by phytoplankton and seaweeds (Dunton 2001, Aumack et al. 2017). The gradient from high to low abundance of seaweeds from the north to the south, i.e. a seaweed density ecotone, may be an important determinant to the trophic ecology of invertebrate communities across the western AP (Cardona et al. 2021, Iken et al. 2023). This is particularly important to understand since ice cover patterns are rapidly shifting as a consequence of climate-driven warming in the region. The trophic ecology of most invertebrate taxa across the hard-to-access subtidal regions of the western AP is not well resolved. Moreover, our understanding of the trophic ecology of most consumers in this system is usually limited to relatively weakly-informative labels such as 'predator', 'scavenger', or 'herbivore'.

In remote and hard-to-access benthic marine ecosystems, elemental and molecular biomarkers are particularly important tools for the study of trophic relationships (Graeve et al. 1994, Budge et al. 2007). Stable isotopes can help resolve differences in basal productivity (^{13}C) and relative trophic position (^{15}N) of consumers (Peterson & Fry 1987, France 1995, Layman et al. 2012). For example, isotopic analyses are regularly used in polar systems to reveal the connections between seaweeds and higher trophic levels (Kaehler et al. 2000, Dunton 2001, Norkko et al. 2007, Zenteno et al. 2019). Across the western AP, it has recently been shown that diverse macroinvertebrate consumers in areas with more ice cover are further removed from macroalgal carbon relative to those in less ice cover (Iken et al. 2023). Not all macroalgal-derived carbon is equal in its quality as food. The seaweed overstory forests of the western AP are dominated by large perennial members of the *Desmarestiales*, which are chemically defended from direct consumption by grazers (Amsler et al. 2008). Multiple *Desmarestia* species can support very high densities of mesograzers, which use the chemically defended structures to seek refuge from predators

(Amsler et al. 2014). These defended seaweeds often host endo-/epiphytic production, which is used by consumers (Aumack et al. 2017). Because of the seaweed chemical defenses, algal-derived detritus generated from the dominant seaweeds along the western AP may not be particularly valuable as a trophic subsidy while fresh, but there is evidence that this carbon does make its way into benthic consumers after the algae have died (Aumack et al. 2017, Ahn et al. 2021).

Fatty acid signature analysis (consisting of >50 different molecules) provides an additional, relatively powerful means for making inferences about resource assimilation by consumers (Dalsgaard & St. John 2004, Pethybridge et al. 2018). Fatty acids are particularly powerful when used in a comparative framework to assess differences in conspecifics among different regions or conditions (Budge et al. 2002, 2007, Galloway et al. 2013). Certain fatty acids can be indicative markers for certain basal producer groups (Graeve et al. 2002, Galloway et al. 2012, Kelly & Scheibling 2012, Galloway & Winder 2015). Moreover, some functional groups of fatty acids are important indicators of ecosystem functioning (Litzow et al. 2006, Budge et al. 2014, Pethybridge et al. 2015) and organismal physiology. For example, polyunsaturated fatty acids (PUFAs) and several ω -3 and ω -6 'essential fatty acids' are only synthesized in biologically relevant amounts by primary producers, and are important for specific biological functions in metazoans, which cannot synthesize these molecules *de novo* (Kainz et al. 2004, Parrish 2009). Organism fatty acids are integrated into tissues by synthesis (in the case of primary producers) or through consumption, modification, and assimilation (in the case of heterotrophs) over varying time scales ranging from weeks to years, depending on growth rates and metabolism (reviewed by Galloway & Budge 2020). Whole fatty acid profile analysis is increasingly used for scaling up our understanding of organismal- to ocean-scale processes using marine ecosystem models (Pethybridge et al. 2018) and comprehensive marine lipidomics (Rey et al. 2022).

Here, we used fatty acid signature analysis to investigate the trophic stability and change of 3 dominant seaweed species and the 8 numerically most dominant macroinvertebrate consumers in diverse trophic guilds and feeding modes across an ice cover and latitudinal gradient of the western AP. We previously characterized the species composition of these same study sites, showing that fleshy macroalgal cover was strongly negatively correlated with increasing ice cover (Amsler et al. 2023), such that sites at the north-

ern (lowest annual mean sea ice cover) end of the gradient had >70% fleshy macroalgal cover, while sites with high ice cover in the south had <1% fleshy macroalgal cover. Moreover, the relative abundance of invertebrate cover was variable along this ice cover gradient. Thus, we hypothesized that the trophic ecology of consumers would differ across this ice gradient and macroalgal ecotone (Fig. 1). Within the context of these gradients in community composition at a large geographic scale, we used both multivariate fatty acid signature analysis and fatty acid functional groups to ask if the fatty acids of seaweeds and macroinvertebrate consumers differed across the ice cover gradient, and to assess the trophic connectivity of consumers to basal macroalgal producers along the western AP. The assumption with these analyses is that the multivariate fatty acid profile of a consumer is affected by diet (Galloway & Budge 2020). Therefore, significant separation in consumer fatty acid signatures across the ice gradient would indicate differences in the trophic resources assimilated by the consumers (Dalsgaard et al. 2003, e.g. Budge et al. 2006) and help clarify how the expected continued reductions in ice cover will alter benthic food webs in this region. Likewise, a lack of differences in fatty acid profiles across the ice gradient is taken to indicate that resource assimilation by consumers does not differ as a result of ice cover.

2. MATERIALS AND METHODS

2.1. Sample collections and preservation

We performed algal and invertebrate sampling at 15 sites across the western AP during a cruise on the Antarctic Research and Support Vessel (ARSV) 'Laurence M. Gould' in the Austral fall, between 23 April and 18 May 2019. We sampled locations between Anvers Island in the north (64.59° S, 64.36° W) and Marguerite Bay in the south (68.69° S, 67.53° W) (Fig. 2). Prior to our cruise, we prepared a list of 41 candidate sites, designed to provide a series of possible replicate dive sites within a wide range of ice gradient characteristics, while being similar in terms of turbidity, substrate, and slope, generally avoiding vertical or steep slopes (e.g. >60°), although this was not measured in advance due to a lack of regional nearshore bathymetric charts. We derived a continuous variable ice cover gradient index from the January–March seasonal means from the Visible Infrared Imaging Radiometer Suite Kd(490) product (following Wang et al. 2017). Seasonal means for the

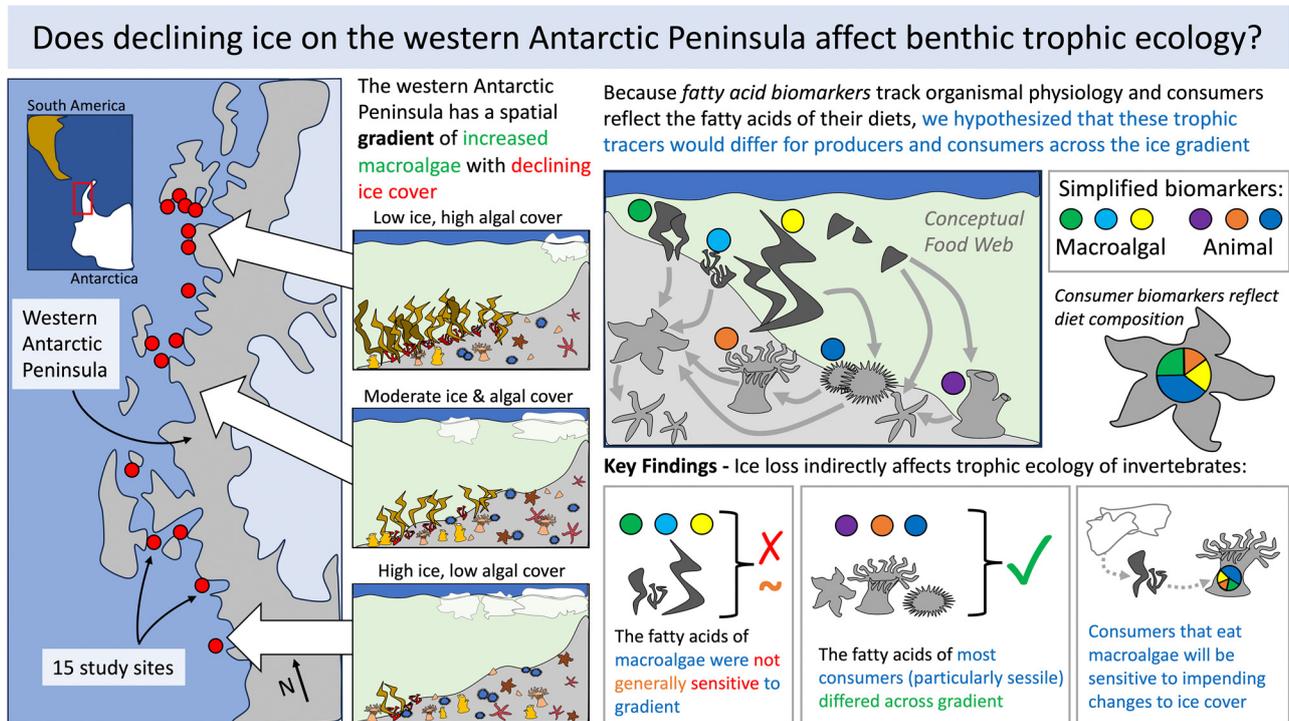


Fig. 1. Summary of the research question, hypothesis, methodology, and key findings

ice index were characterized by their annual (12 mo) mean sea ice concentrations for the weekly National Ice Center (NIC) ice charts from 2015–2018, as justified and described in detail in Appendix S3 in Amsler et al. (2023). The final sites were designated A–N following a north to south gradient, except for site X, which was an additional site with shallow, relatively flat topography (7–10 m depth) only sampled for the isotopic and fatty acid biomarker components of our projects. The ice indices were assigned to each study site prior to analysis (Fig. 2). Because high-definition bathymetric charts are not generally available for most nearshore areas in this region, final decisions about actual locations of surveys had to be made immediately prior to dive surveys during scouting trips.

The ARSV 'Gould' transited throughout the range of our possible study sites for 25 d. The SCUBA survey methods are described in detail by Amsler et al. (2023). Briefly, the ARSV 'Gould' would navigate to within ~5 km of the candidate dive sites, and hold on station while 3 dive teams rotated onto the dive sites using 5 m zodiacs. At each site, 3 replicate video transects, separated by ~100 m, were surveyed by dive teams, from 40 to 5 m depth, in a zig-zag ladder design. Surveys captured high-definition video paired with laser scalers to enable calculation of area surveyed, and collections were made at 5 m depth in-

crements from 35 to 5 m. Follow-up dives sampled across the replicate video transects at the site level and focused on haphazard collections of common macroinvertebrates and macroalgae. At 4 sites (B, E, G, and I), we also opportunistically collected surface scrapes of benthic microalgal diatom clumps, which were clearly visible as mats on otherwise unvegetated, soft sediments. The SCUBA sampling protocol therefore allowed us to quantify percent cover of large benthic algal and invertebrate spaceholders, as well as high-definition presence/absence data for seaweeds, which were the primary focus of the study. Due to limitations in SCUBA bottom time at each site, collections and surveys could not provide measurements of biomass of algal or invertebrate standing stock.

Upon return to the ARSV 'Gould' research labs, samples were held in a flow-through seawater aquarium and in coolers with seawater until processing on the same day. Vouchers of all species sampled were retained for later morphological and/or DNA-based confirmation, and taxon names were unified following the World Register of Marine Species (WoRMS Editorial Board, <https://www.marinespecies.org/>). When possible, we preserved tissues from at least 5 replicate individuals of each species for fatty acid analysis. We sampled the same tissue type for each alga (avoiding meristem and reproductive tissues) and invertebrate

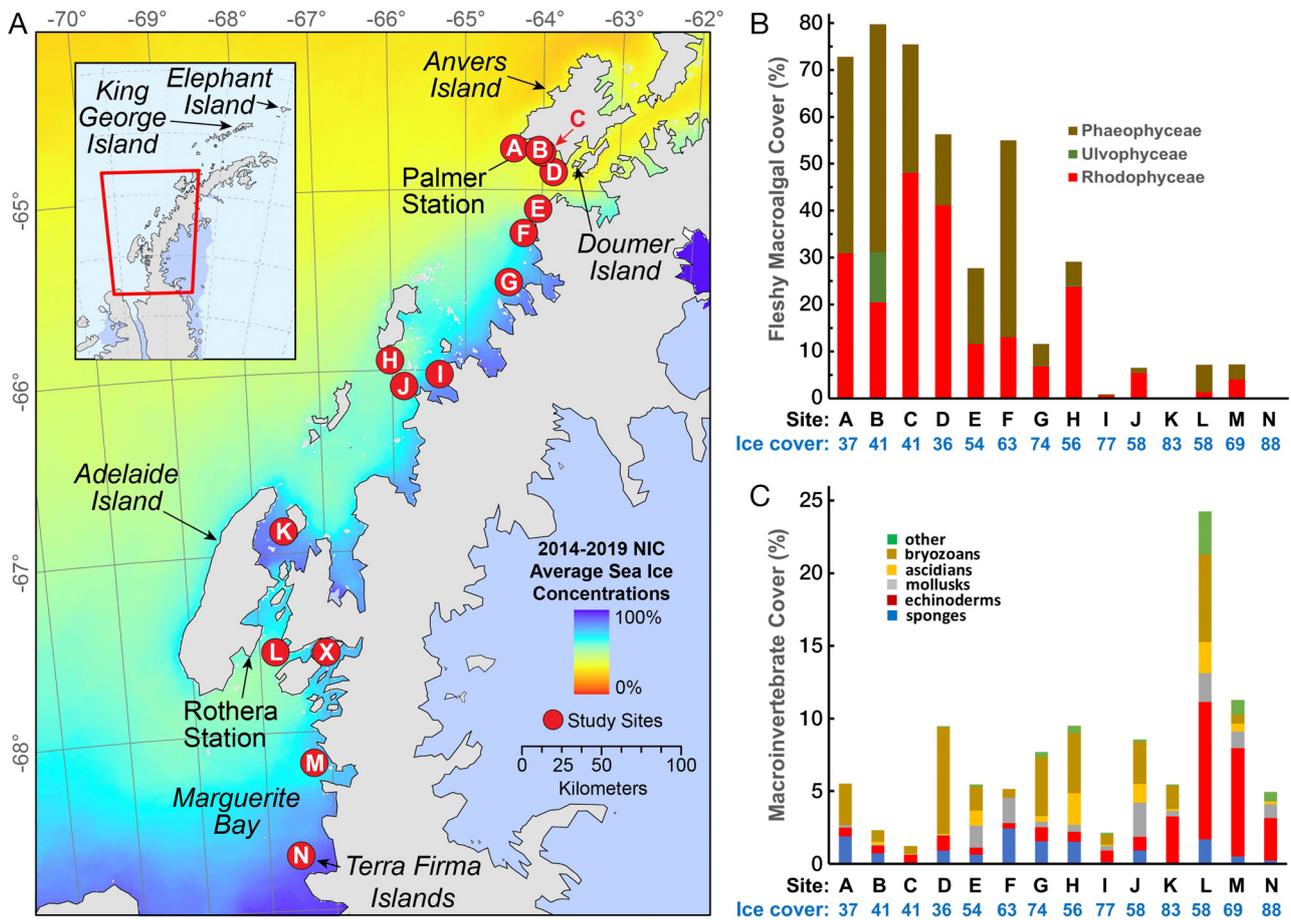


Fig. 2. Study area and relationships between macroalgal cover and correlation with sea ice cover, redrawn from Amsler et al. (2023). (A) Sampling sites (A–N, X) along the western Antarctic Peninsula. The 2014–2019 National Ice Center (NIC) average sea ice concentrations are modeled with the heat ramp (see Section 2). Light purple areas show ice cover to the East of the Peninsula for which ice cover is not modeled. (B) Mean percent benthic cover of 3 macroalgal groups (Phaeophyceae, Ulvophyceae, Rhodophyceae) at the 15 study sites. (C) Mean percent benthic cover of 6 broad taxonomic groups of invertebrates. Site codes are shown in black letters and the NIC ice cover (annual, %) from Amsler et al. (2023) is shown in blue

(generally focusing on muscle tissue, when possible). Samples were stored in 2.0 ml Eppendorf tubes and frozen at -80°C within minutes of removal from seawater. Here, we focused on the most common algae and invertebrates that were found in at least 8 (macroalgae) or 9 (macroinvertebrates) sites surveyed in the gradient, for which we also had a minimum of 2 replicates at each site. The full list of taxa, including full species names, modality, collection sites, and tissue types sampled, is presented in Table 1. After the first use of the full species names, subsequent reference to that taxon is only to the genus. Companion articles focused on the species composition and general biogeographical patterns (Amsler et al. 2023), a combined fatty acid and isotopic analysis of a larger suite of all algae sampled on the cruise (Whippo 2023, Whippo et al. 2024), and an isotopic analysis of a comprehensive macroinvertebrate consumer list (Iken et

al. 2023). There was not always enough tissue for aliquots to be allocated to all studies, which accounts for why the exact number of sites used in analyses may differ between studies.

2.2. Fatty acid analysis

Frozen samples were shipped on dry ice to the University of Oregon Institute of Marine Biology in August 2019, and transferred to a -80°C freezer until processing. All samples used in this analysis were processed within 1 yr of collection. Prior to extraction of fatty acids, samples were lyophilized to total dryness, then ground to a homogeneous powder using a stainless steel mortar and pestle. Depending on tissue type, $\sim 5\text{--}40$ mg of material (low end: urchin gonad, high end: seaweeds) were weighed and placed in a

Table 1. Summary of organisms sampled for fatty acids analysis. Site codes and corresponding ice index are presented in Fig. 2 and Amsler et al. (2023). Icon images from PhyloPic 2023 are not generally exact species matches but are meant to be a visual aid for basic body plans (<https://www.phylopic.org/permalinks/d2aeac4501f3f5d91a88051f3ac66f32e454c092b5741593e41dd27df125175a>)

| Group | Icon | Genus species | Phylum | Modality | Sites Analyzed (total) and <i>List</i> | Tissue used |
|--------|---|--------------------------------|---------------|----------|--|-------------|
| Algae |  | <i>Desmarestia menziesii</i> | Ochrophyta | sessile | (12) A-C, E-G, I-N | Thallus |
| |  | <i>Iridaea cordata</i> | Rhodophyta | sessile | (10) A-G, I, J, M | Thallus |
| |  | <i>Plocamium</i> sp. | Rhodophyta | sessile | (8) A-G, J | Thallus |
| Invert |  | <i>Cnemidocarpa</i> sp. | Chordata | sessile | (14) A-H, J-N, X | Body wall |
| |  | <i>Dendrilla antarctica</i> | Porifera | sessile | (11) A-G, J, L-N | Body |
| |  | <i>Isotealia antarctica</i> | Cnidaria | sessile | (9) E-H, J-M, X | Body wall |
| |  | <i>Nacella concinna</i> | Mollusca | mobile | (15) A-N, X | Foot |
| |  | <i>Neosmilaster georgianus</i> | Echinodermata | mobile | (10) A-H, J, M | Arm tip |
| |  | <i>Odontaster validus</i> | Echinodermata | mobile | (15) A-N, X | Arm tip |
| |  | <i>Perknaster aurorae</i> | Echinodermata | mobile | (11) A-G, J, L-M, X | Arm tip |
| |  | <i>Sterechinus neumayeri</i> | Echinodermata | mobile | (12) A, E-N, X | Gonad |

10 ml centrifuge tube, then mixed with a chloroform:methanol (2:1) solution. We used nondecanoic acid (C19) as an internal standard due to its naturally low concentrations in marine samples. After adding the C19 standard, the sample was flushed with nitrogen, sonicated in an ice-water bath, and centrifuged at 3000 rpm ($1711 \times g$) (5 min at 4°C). The chloroform/organic layer containing the dissolved lipids was then transferred to a new 8 ml scintillation vial. This process was repeated twice before evaporating the organic layer under nitrogen down to 1.5 ml. A 1 ml aliquot of this layer was then removed for transesterification and the remaining 0.5 ml of material was preserved at -80°C for later gravimetry (Taipale et al. 2016, Schram et al. 2018).

To begin the transesterification of fatty acids, 1 ml of toluene and 2 ml of 1% sulfuric acid:methanol solution were added to the lipid extract. Samples

were then heated in a water bath for 90 min at 90°C . After transesterification, samples were left to cool to room temperature before adding 2 ml of hexane and 1.5 ml of sodium bicarbonate. The sample was vortexed for 10 s and centrifuged for 2 min at 1500 rpm ($428 \times g$) at 4°C. The fatty acid methyl esters (FAMES) in the upper layer were isolated and evaporated under nitrogen, and re-suspended for a second time by adding 1.5 ml of hexane, evaporated to dryness, and then transferred to a gas chromatograph vial for analysis (Taipale et al. 2016, Schram et al. 2018). FAMES were later identified using a gas chromatograph mass spectrometer (Model QP2020, Shimadzu) following Schram et al. (2018). After removing trace (those with $<0.5\%$) fatty acids, the reduced data set of 50 remaining fatty acids was re-standardized to 1.0 (i.e. 100%) prior to analyses (Kelly & Scheibling 2012).

2.3. Data analysis

We evaluated multivariate fatty acid profiles using a series of routines available in Primer v6.1.13 with PERMANOVA+ v.1.0.3 (Clarke & Gorley 2006, Anderson et al. 2008). To test for differences among sites, we used 1-way permutational multivariate analysis of variance (PERMANOVA; Type III SS, unrestricted permutation of the raw data, site as fixed effect), followed by pairwise comparisons, and 1-way permutational homogeneity of dispersions (PERMDISP), to test for differences and dispersion in fatty acid signatures of each taxon on the categorical variable 'site'. Distance-based linear models (DISTLM) then tested the explanatory power (R^2) of the continuous ice index variable (NIC—annual, as per Amsler et al. 2023) on the multivariate fatty acid signatures of all 11 target taxa. All Primer analyses used Euclidean distance resemblance matrices calculated on the fatty acid compositional data, and all analyses were run with 9999 permutations. We used non-metric multidimensional scaling (nMDS) for visualizing these analyses. To assess the relative differences in site-level distinctiveness among taxa, we also summarized the total number and percentage of the PERMANOVA pairwise tests, which were significant in this analysis.

Analyses of site effects and ice gradient effects were focused on each taxon individually because of the well-known strong differences in fatty acid compositions of different consumer and algal taxa. Because of the extreme gradient in algal species distribution and abundance across the ice and biogeographical gradient sampled, we could not meaningfully analyze the effects of ice cover for more than 3 algal species. However, for the sake of interpretations of all consumer fatty acid signatures in the context of the producers, we also present one nMDS analysis showing fatty acid vector overlays that had >0.5 Pearson correlation with the nMDS axes. This analysis also includes additional basal 'end members' that were not found in sufficient abundance with enough replication to analyze across all sites, including opportunistically sampled benthic diatoms (4 sites) and the brown alga *Himanthothallus grandifolius* (which was collected at 8 sites, but unfortunately without sufficient within-site replication for analysis). Including these taxa as potential end members provides reference orientation of the dominant taxa within major sources of basal benthic productivity (red and brown fleshy macroalgae and diatoms) across the study area. Our focus was on benthic production, as we did not sample phytoplankton for fatty acids analysis.

We summarized fatty acid variables into 5 categories following commonly used functional groups and source biomarker variables: saturated (SAFA), mono-unsaturated (MUFA), and PUFA; bacterial (all odd carbon length); and a commonly used diatom (16:1 ω 7) marker. It is important to note that the latter fatty acid is common in all diatoms as a group (Kelly & Scheibling 2012), and cannot on its own differentiate sea ice, pelagic, or benthic diatoms. Other summary groups such as long-chain essential fatty acids or brown algal markers (which are mostly PUFAs) were not used because they were largely redundant to the PUFA summary category. We correlated univariate fatty acid summary and biomarker variables for each taxon with the NIC annual mean sea ice (% cover) derived for each study site. All multivariate and univariate test p-values were interpreted as significant (*) at $p < 0.05$ and considered as highly significant (**) at $p < 0.005$. For mean annual sea ice concentrations of the sites actually visited, 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, as described by Iken et al. (2023) and Amsler et al. (2023). Univariate analyses were performed and visualized with R (R Core Team 2022) using the packages 'broom' (Robinson 2023), 'dplyr' (Wickham et al. 2023), and 'ggplot2' (Wickham 2016).

3. RESULTS

3.1. Multivariate fatty acid signature analysis

An nMDS ordination of all focal taxa analyzed across the ice gradient, plus several additional algal taxa for reference, shows the most important 18 fatty acids that had >0.5 Pearson correlations with the nMDS axes as blue vector overlays (Fig. 3). The length of the vector is proportional to the Pearson correlation value. The nMDS shows the algal groups (all in light gray) occupying 3 of the 4 corners of the plot, with the dominant red macroalgae *Iridaea cordata* and *Plocamium* sp. in the upper left corner, benthic diatoms in the upper right corner, and the dominant brown macroalgae *Himanthothallus* and *Desmarestia menziesii* in the lower right. The long-chain essential fatty acid (LCEFA) 20:5 ω 3 (eicosapentaenoic acid, EPA), a commonly used biomarker for red algae generally, is strongly associated with red algae at the upper and left side of the nMDS. The MUFA 16:1 ω 7, a diatom biomarker, and the SAFAs 14:0 and 16:0 are associated with the upper right areas of the plot. The lower portion of the plot, where the brown algae

reside, is associated with several of the primary biomarkers for brown algae, including the essential fatty acids 18:3 ω 3 (alpha-linolenic acid, ALA), 18:4 ω 3 (stearidonic acid, SDA), and 20:4 ω 6 (arachidonic acid, ARA).

As is generally expected from fatty acid signature analysis of diverse taxonomic groups, the heterotrophic consumers are oriented within the inner space of the ordination between the producer groups, and are within this inner space grouped with more closely related organisms. All 3 sea stars (in shades of blue), i.e. *Neosmilaster georgianus*, *Odontaster validus*, and *Perknaster aurorae*, occupy the lower left corner of the plot, with the latter species having significantly high multivariate dispersion (Table 2). All sea stars are associated with ARA, 2 MUFAs (20:1 ω 9, 20:1sum), and the SAFA 18:0. The other echinoderm, the sea urchin *Sterechinus neumayeri*, has moderately large dispersion and is central in the ordination, and therefore does not have any strong affiliation with any particular fatty acids, but is associated on the right side of the ordination with 16:1 ω 7 and the LCEFA 22:6 ω 3 (docosahexaenoic acid, DHA).

Other consumers in the central and right sides of the ordination are the tunicate *Cnemidocarpa* sp. and the sponge *Dendrilla antarctica*, both associated with DHA, 16:1 ω 7, 16:0, and 14:0. Aside from 3 outliers, which are far from the group centroid, the *Cnemi-*

docarpa sp. samples have moderately small dispersion, and *Dendrilla* has the smallest amount of fatty acid dispersion. *Dendrilla* is also associated with the bacterial fatty acid marker i15:0, the SAFAs 20:0, 22:0, and 2 of the brown algal markers (ALA, SDA). The

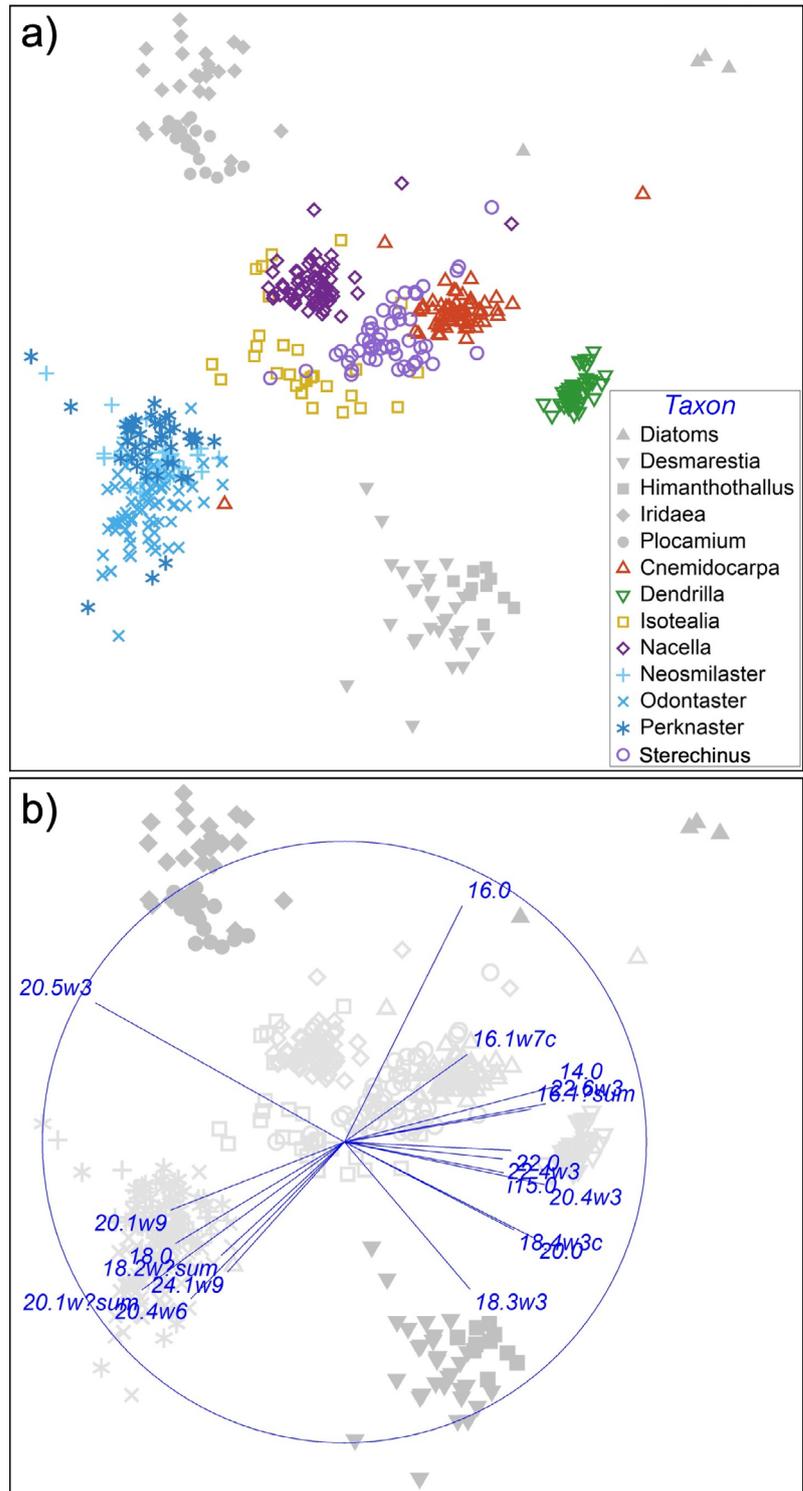


Fig. 3. Non-metric multidimensional scaling (nMDS) visualization of fatty acid signatures of study taxa (50 fatty acids), Euclidean distance, 2D stress = 0.13. (a) nMDS plot of 5 dominant algae (gray symbols; Rhodophyta in upper left, diatoms in upper right, Ochrophyta in lower right) and 8 macroinvertebrates (colored symbols), which were found in at least 9 of the 15 study sites along the western Antarctic Peninsula, showing the taxonomic grouping of the samples by phylogenetic relationships (see Table 1). (b) Same ordination as in panel (a), but all samples are gray (darker for algae, lighter for invertebrates) to allow clarity for visualizing fatty acid vector overlays, showing the n = 18 fatty acids that had >0.5 Pearson correlations with nMDS axes 1 and 2

Table 2. Summary of multivariate analyses on the fatty acid (FA) signatures (% composition of 50 FAs) of the 10 taxa (2 seaweeds and 8 invertebrates) sampled across the gradient at a minimum of 8 and 9 sites for seaweeds and invertebrates, respectively. Descriptions of the PERMANOVA, PERMDISP, and DISTLM tests are provided in Section 2. Reported degrees of freedom (df) for the tests may be less than the number of sites collected – 1 (Table 1) if only 1 sample was ultimately analyzed from a site. The explanatory power (R^2) of the continuous ice index variable is also reported from the DISTLM analyses. All p-values reported in the table are interpreted as significant (*) at $p < 0.05$ and highly significant (**) at $p < 0.005$ (highlighted in **bold**)

| Genus | df | 1-way PERMANOVA on site p(MC) | Significant PERMANOVA pairwise comparisons on site [n (%)] | 1-way PERMDISP on site p(perm) | DISTLM test of ice gradient on FA signatures p | FA variation explained by ice gradient in DISTLM (R^2), % |
|---------------------|----|-------------------------------|--|--------------------------------|--|---|
| <i>Desmarestia</i> | 11 | 0.0188* | 5 (7.6) | 0.7247 | 0.0077* | 10.9 |
| <i>Iridaea</i> | 9 | 0.0001** | 19 (43.2) | 0.0771 | 0.0291* | 11.8 |
| <i>Plocamium</i> | 7 | 0.0003** | 7 (25.0) | 0.6355 | 0.0566 | 12.8 |
| <i>Cnemidocarpa</i> | 12 | 0.0001** | 65 (83.3) | 0.6007 | 0.0003** | 9.4 |
| <i>Dendrilla</i> | 10 | 0.0001** | 50 (90.9) | 0.1252 | 0.0001** | 35.8 |
| <i>Isotealia</i> | 8 | 0.0001** | 31 (86.1) | 0.3272 | 0.0004** | 17.2 |
| <i>Nacella</i> | 14 | 0.0001** | 68 (64.8) | 0.4243 | 0.0132* | 5.2 |
| <i>Neosmilaster</i> | 9 | 0.0001** | 34 (75.6) | 0.0480* | 0.0150* | 7.0 |
| <i>Odontaster</i> | 14 | 0.0001** | 51 (48.6) | 0.1155 | 0.0020** | 6.8 |
| <i>Perknaster</i> | 10 | 0.0001** | 35 (63.6) | 0.0002** | 0.0664 | 6.0 |
| <i>Sterechinus</i> | 11 | 0.0001** | 40 (60.6) | 0.0297* | 0.0004** | 10.4 |

gastropod *Nacella concinna* is in the upper central part of the plot, has a generally low dispersion, and is most closely aligned with the red algae (upper left) and diatoms (upper right). The fatty acids most associated with *Nacella* are EPA, 16:0, and 16:1 ω 7. The anemone *Isotealia antarctica* has moderately large dispersion and is centrally located in the ordination.

3.2. Site and ice-gradient analyses

Table 2 summarizes the p-values for statistical tests, the number and % of sites with significant differences in post hoc PERMANOVA tests, and the DISTLM R^2 values showing the percentage of the total variation in fatty acid signatures for each taxon explained by the ice gradient data. A summary of the correlations between univariate fatty acid summary categories and specific biomarkers with ice cover is shown in Table 3 and Fig. 4. The full statistical results tables for the PERMANOVA, PERMDISP, and DISTLM tests are reported in Tables S1–S3, respectively, in the Supplement 1 at www.int-res.com/articles/suppl/m735p043_suppl1.pdf. The complete fatty acids percentage dataset used in this analysis is shared in Supplement 2 at www.int-res.com/articles/suppl/m735p043_suppl2.csv.

3.2.1. Seaweeds

Fatty acids of *Desmarestia menziesii* differed across sites, but pairwise tests showed that only 7.6% of sites

differed from each other. The ice gradient explained a significant amount (10.9%) of the variance in the fatty acid composition of *Desmarestia* (DISTLM). *Iridaea cordata* fatty acids differed across sites, and pairwise PERMANOVA tests revealed that 43.2% of sites differed from each other, the highest for any alga. The ice gradient explained a significant amount (11.8%) of the variance in the fatty acid composition of *Iridaea* (DISTLM). Fatty acid signatures of *Plocamium* sp. differed across sites, and pairwise tests found that 25.0% of sites differed from each other. The ice gradient was not significant (DISTLM), and explained 12.8% of the variance in the fatty acid composition in *Plocamium*. The fatty acid signatures of the brown alga *Desmarestia* and the red alga *Plocamium* had very low multivariate dispersion, and the red alga *Iridaea* had higher (albeit still non-significant) multivariate dispersion (Table 2).

An nMDS visualization of *Desmarestia*, *Iridaea*, and *Plocamium* fatty acid signatures as coded by study site and ice gradient (Fig. S1 in Supplement 1), shows that there are no consistent groupings or gradients in multivariate space related to the gradient of ice cover. Because of the relatively small number of sites where sufficient replicate samples of *Himanthothallus* and benthic diatoms were collected, which were all additionally constrained to the northern sites (A–F), we did not analyze differences for these taxa, but they are presented in Fig. 3 as possible reference producer end-points only. In the seaweeds, PUFA contents were consistently high, and SAFAs and MUFAs were variable. No specific marker or fatty acid summary

Table 3. Summary of correlations between univariate fatty acid (FA) summary categories (SAFA: saturated; MUFA: mono-unsaturated; PUFA: polyunsaturated; bacterial: all odd carbon length FAs; diatom marker: 16:1 ω 7) and (%) and National Ice Center sea ice cover (annual%). For each taxon, residual degrees of freedom (df), R^2 , and p-values are shown, and all p-values reported in the table are interpreted as significant (*) at $p < 0.05$ and highly significant (**) at $p < 0.005$ (highlighted in bold)

| Genus | df | SAFA | | MUFA | | PUFA | | Bacterial FA | | Diatom FA | |
|---------------------|----|-------|---------------------|-------|---------------------|-------|---------------------|--------------|-----------------|-----------|---------------------|
| | | R^2 | p | R^2 | p | R^2 | p | R^2 | p | R^2 | p |
| <i>Desmarestia</i> | 30 | 0.06 | 0.1869 | 0.09 | 0.1000 | 0.14 | 0.0319* | 0.00 | 0.7100 | 0.02 | 0.4420 |
| <i>Iridaea</i> | 23 | 0.12 | 0.0930 | 0.01 | 0.5810 | 0.11 | 0.1029 | 0.00 | 0.7620 | 0.00 | 0.8905 |
| <i>Plocamium</i> | 19 | 0.10 | 0.1547 | 0.13 | 0.1084 | 0.01 | 0.7016 | 0.03 | 0.4545 | 0.14 | 0.0990 |
| <i>Cnemidocarpa</i> | 60 | 0.01 | 0.5532 | 0.03 | 0.1782 | 0.01 | 0.3697 | 0.00 | 0.5965 | 0.03 | 0.1941 |
| <i>Dendrilla</i> | 46 | 0.31 | <0.0001** | 0.43 | <0.0001** | 0.01 | 0.4583 | 0.03 | 0.2159 | 0.53 | <0.0001** |
| <i>Isotealia</i> | 28 | 0.23 | 0.0076* | 0.39 | 0.0002** | 0.11 | 0.0691 | 0.00 | 0.9048 | 0.01 | 0.6630 |
| <i>Nacella</i> | 67 | 0.10 | 0.0082* | 0.23 | <0.0001** | 0.00 | 0.6171 | 0.02 | 0.1980 | 0.02 | 0.3011 |
| <i>Neosmilaster</i> | 43 | 0.10 | 0.0309* | 0.08 | 0.0544 | 0.00 | 0.7033 | 0.07 | 0.0840 | 0.06 | 0.1027 |
| <i>Odontaster</i> | 68 | 0.00 | 0.9355 | 0.36 | <0.0001** | 0.33 | <0.0001** | 0.00 | 0.7811 | 0.11 | 0.0060* |
| <i>Perknaster</i> | 40 | 0.01 | 0.5369 | 0.06 | 0.1090 | 0.05 | 0.1568 | 0.00 | 0.6587 | 0.24 | 0.0010** |
| <i>Sterechinus</i> | 49 | 0.08 | 0.0401* | 0.23 | 0.0003** | 0.10 | 0.0222* | 0.15 | 0.0048** | 0.20 | 0.0011** |

categories in either algal taxon correlated with ice cover (Table 3, Fig. 4).

3.2.2. Invertebrates

In general, all taxa except *Perknaster* had low multivariate dispersion of fatty acid signatures between sites (PERMDISP, Table 2; Table S2). The fatty acid signatures of all invertebrate taxa differed across sites (1-way PERMANOVA, Table 2; Table S1), and 50% of those taxa also showed evidence of differences in site due to the ice gradient. In the invertebrates, there was moderate variation between taxa on the number of significant post hoc test comparisons between sites, ranging from a low of 48.6% (*Odontaster*) to a high of 90.9% (*Dendrilla*) (Table 2). The nMDS plots showing the fatty acid signatures of all invertebrates are provided in Fig. S2. *Cnemidocarpa* fatty acid signatures differed across the ice gradient, and ice cover explained 9.4% of the total variation in the DISTLM analysis. *Cnemidocarpa* fatty acid signatures differed among 83% of all sites (Fig. S2a). *Cnemidocarpa* did not have any significant correlations between univariate fatty acid variables and ice cover (Fig. 4, Table 3). *Dendrilla* fatty acid signatures differed across the ice gradient, and ice cover explained 35.8% of the total variation in the DISTLM analysis. Notably, this is twice the level of variation explained by the ice gradient than any other species. *Dendrilla* fatty acid signatures differed among 90.9% of all sites (Fig. S2b). Total MUFAs and the diatom marker 16:1 ω 7 were both positively correlated and total SAFA was negatively correlated with increased ice cover in *Den-*

drilla (Fig. 4, Table 3). *Isotealia* fatty acid signatures differed across the ice gradient, and ice cover explained 17.2% of the total variation in the DISTLM analysis. *Isotealia* fatty acid signatures differed among 86.1% of all sites in post hoc analyses (Fig. S2c). Total MUFA was negatively correlated with increased ice cover in *Isotealia* (Fig. 4, Table 3). *Nacella* fatty acid signatures did not differ across the ice gradient, and the DISTLM found that ice cover explained only 5.2% of the total variation, the lowest variation explained by the ice gradient in any species. *Nacella* fatty acid signatures differed among 64.8% of all sites in post hoc analyses (Fig. S2d). Total MUFA was positively correlated with increased ice cover in *Nacella* (Fig. 4, Table 3). *Neosmilaster* fatty acid signatures did not differ across the ice gradient, and the DISTLM found that ice cover explained 7.0% of the total variation. *Neosmilaster* fatty acid signatures differed among 75.6% of all sites in post hoc analyses (Fig. S2e). *Neosmilaster* did not have any significant correlations between univariate fatty acid variables and ice cover (Fig. 4, Table 3). *Odontaster* fatty acid signatures differed across the ice gradient, although ice cover explained only 6.8% of the total variation in the DISTLM analysis. *Odontaster* fatty acid signatures differed among 48.6% of all sites in post hoc analyses (Fig. S2f). Total MUFA was positively correlated and total PUFA was negatively correlated with increased ice cover in *Odontaster* (Fig. 4, Table 3). *Perknaster* fatty acid signatures did not differ across the ice gradient, and the DISTLM found that ice cover explained only 6.0% of the total variation. *Perknaster* fatty acid signatures differed among 63.6% of all sites in post hoc analyses (Fig. S2g), and 16:1 ω 7 was positively correlated with

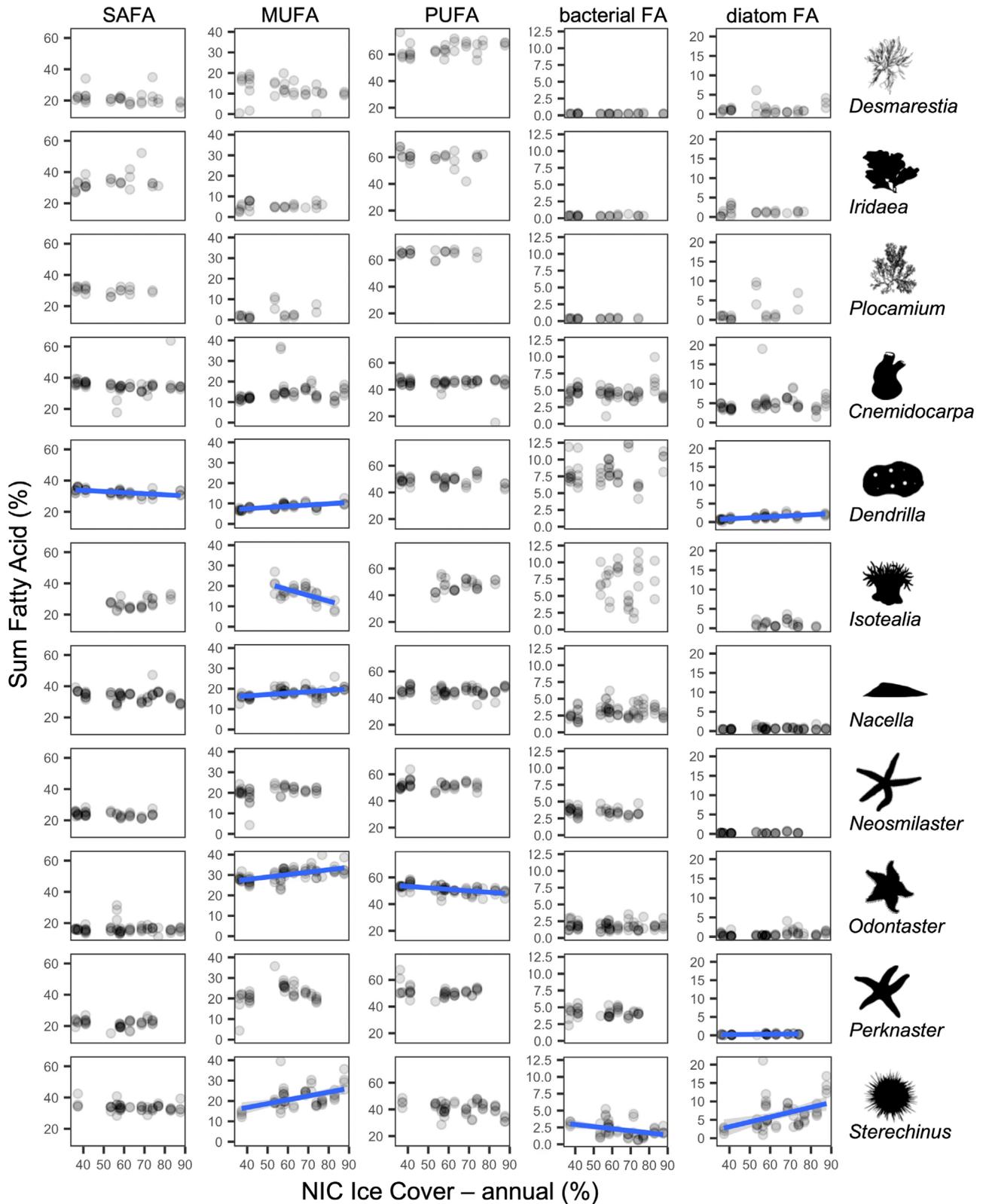


Fig. 4. Univariate correlations between summary categories fatty acid (FA) percentages (columns) and annual National Ice Center (NIC) ice cover percentage (calculated in Amsler et al. 2023) for the 11 organisms (rows) found at sufficient sites (see Section 2) across the ice gradient. Blue regression lines show significant relationships. The FA functional groups and summary categories are: SAFA: saturated; MUFA: monounsaturated; PUFA: polyunsaturated; bacterial FA: the sum of bacterial fatty acids (odd carbon length molecules); diatom FA: 16:1 ω 7, a diatom marker FA. Points on the plots are set at a uniform transparency of grey to reduce overplotting; darker looking points are the result of multiple overlapping points at the same or very similar locations on the plot

increased ice cover in *Perknaster* (Fig. 4, Table 3). *Sterechinus* fatty acid signatures differed across the ice gradient, and ice cover explained 10.4% of the total variation in the DISTLM analysis. *Sterechinus* fatty acid signatures differed among 60.6% of all sites in post hoc analyses (Fig. S2h). Total MUFA and 16:1 ω 7 was strongly positively correlated and bacterial fatty acids were negatively correlated with increased ice cover in *Sterechinus* (Fig. 4, Table 3).

4. DISCUSSION

We sampled the largely uncharted and understudied nearshore waters of the archipelago and fjords of the western AP, visiting rocky subtidal sites across $>4^\circ$ of latitude, most of which have never been studied. Because of the large variation in the macroalgal cover along the western AP, which ranges from $>75\%$ in the north to $\sim 0\%$ in the south (Fig. 2), we hypothesized that the fatty acids of cosmopolitan invertebrate consumers of the AP would differ between sites, but particularly between the north and the south following an increasing gradient of annual sea ice cover. Our results identify several general patterns in the trophic ecology of benthic consumers along the western AP. All sessile consumer fatty acids changed significantly with sea ice cover, whereas the fatty acid signatures of the majority (3 of 5) mobile consumers did not differ across the gradient. Specifically, we found support for the ice gradient ecotone hypothesis for 5 out of the 8 invertebrates: *Cnemidocarpa* sp. (tunicate; sessile suspension feeder); *Dendrilla antarctica* (sponge; sessile suspension feeder); *Isotealia antarctica* (anemone; sessile predator); *Odontaster validus* (sea star; mobile scavenger), and *Sterechinus neumayeri* (sea urchin; mobile scavenger and grazer). We did not find support for an ice gradient ecotone hypothesis for 2 of the (mobile) sea stars, *Neosmilaster georgianus* and *Perknaster aurorae* (both considered to be both scavengers and predators), and *Nacella concinna* (gastropod; mobile grazer and generalist). We documented significant general site-level differentiation in the fatty acid signatures for all 8 invertebrates. *Odontaster* exhibited the least overall site-level differences among study sites, but even in this case, pairwise comparisons showed that 48.6% of sites still differed in their fatty acid signatures. These site-level differences found in the fatty acids of all organisms may have been driven by factors that influence trophic ecology of the consumers or fatty acid biosynthesis. For example, we were not able to analyze factors such as turbidity, ice scour, or open water or ice-

associated productivity. There also was considerable variation in the biological community composition of these study sites (Amsler et al. 2023), which likely affects local trophic dynamics of benthic consumers.

Rapidly warming polar regions (Smetacek & Nicol 2005) are creating the potential for major changes in polar seaweed-dependent communities. General texts (Wiencke & Bischof 2012) and reviews (Müller et al. 2009, Harley et al. 2012) on the subject of climate change effects on seaweed biology and ecosystems have focused on the possible impacts of stressors on seaweeds such as ocean acidification and warming. However, along the western AP, it is increasingly clear that changes to sea ice cover and the resulting increases in light availability are the most important changes occurring with respect to seaweeds, and that expected changes will provide favorable conditions for range expansion and increased biomass for benthic seaweeds (McClintock et al. 2008, Wiencke & Amsler 2012, Amsler et al. 2023). It stands to reason that reorganization of benthic communities as a result of changes in seaweed cover is also likely to alter the invertebrate communities (Clark et al. 2015). A pressing question is whether and how such changes will affect the trophic ecology and community composition of the shallow nearshore Antarctic benthos. The corresponding stable isotope analysis along this sea ice gradient suggests that food webs will become more complex and more dependent on the larger diversity of macroalgae with decreasing sea ice cover (Iken et al. 2023). However, all of the invertebrate consumers evaluated in the present study are relatively poorly understood in terms of their trophic ecology, and almost nothing is known about the lipid metabolism in these consumers. Thus, fatty acid signature analysis provides a novel and powerful biomarker approach for identifying unknown pathways of energy flow in this understudied system.

Our analysis helps clarify the trophic importance of basal production by seaweeds, whether indirectly or directly, to consumer taxa even though they use different strategies to obtain sustenance, and may occupy different trophic guilds. For example, the sponge *Dendrilla* and the anemone *Isotealia* were the 2 taxa with the largest percent of their total fatty acid signature variation explained by the ice cover gradient (through DISTLM). The tunicate *Cnemidocarpa* also exhibited moderately high and significant variation of its fatty acid signature explained by ice cover. All 3 of these sessile taxa exhibited the highest content and largest variability in their total bacterial fatty acids (Fig. 4), but the reason for this is still unclear, and there were no consistent correlations be-

tween total bacterial fatty acids and ice cover for any consumer except for *Sterechinus*. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Dendrilla* and *Cnemidocarpa* were related to sea ice cover at the same sites in our companion isotope biomarker study (Iken et al. 2023). *Cnemidocarpa* has been shown to assimilate macroalgal-derived carbon and resuspended benthic material in the northern part of the western AP (Tatián et al. 2004, 2008). Antarctic benthic suspension feeders are well poised to efficiently take advantage of a wide diversity of prey (Gili et al. 2001). However, *Isotealia* is not just a passive suspension feeding anemone; it is a known predator of the sea urchin *Sterechinus* (Amsler et al. 1999), although it is unknown how commonly this approach to ambush predation is employed. *Isotealia* fatty acid signatures also varied considerably with the ice cover and macroalgal cover gradient, suggesting that it either consumes prey that eat macroalgae, or that it directly consumes detritus when it has the chance to. The multivariate fatty acid signatures of *Isotealia* did overlap considerably with the sea urchin (Fig. 3), but it did not incorporate some of the specific fatty acid patterns of *Sterechinus* such as increased diatom biomarker accumulation in high ice areas.

The multivariate fatty acid signatures of seaweeds differed among sites, but were not, apart from *Desmarestia*, generally as sensitive to the ice gradient as the consumers (e.g. Fig. S1). Other studies, using isotopes as biomarkers, have also found varying results with negligible to small variation in the isotopic values of seaweeds across the same geographic scale on the western AP (Iken et al. 2023), but also see Cardona et al. (2021), who sampled during the austral summer and did find changes in the isotopic baseline of producers. The seaweeds in the present study had consistently high proportions of PUFAs (e.g. generally >55%), a pattern noted in the fatty acid profiles of several other Antarctic macroalgae (Graeve et al. 2002, Whippo et al. in press). The relative algal % PUFA levels were consistently higher than the invertebrates, and no fatty acid category or marker varied across the ice gradient in the seaweeds, except for *Desmarestia*, which had a slight increase in % PUFAs at higher ice cover sites. This implies that with respect to lipids, future declines in ice cover will not substantively affect the nutritional value of these algae, and the expected range expansion will be a novel source of lipids to previously ice-dominated habitats. Few studies have evaluated site-level variation in seaweed fatty acids (e.g. Britton et al. 2021), but research on other taxa has demonstrated that irradiance can affect fatty acid composition (Floreto & Teshima 1998,

Khotimchenko & Yakovleva 2004, Guschina & Harwood 2009). The lack of systematic differences in both univariate fatty acid summary categories and multivariate fatty acid signatures of the algae in our study, which are subject to a large range in seasonal ice cover and total annual irradiance, is puzzling and in need of further mechanistic study. To our knowledge, the question of site-level variation in algal or consumer lipids, particularly in the context of climate change, has not been addressed in Antarctic algae or macroinvertebrates.

The fatty acid signatures of the cosmopolitan sea urchin *Sterechinus* differed strongly across the ice gradient and between sites. *Sterechinus* had a relatively large multivariate fatty acid dispersion (albeit not statistically significant), implying that a wide range of trophic resources support this consumer across the ice cover gradient. There was strong evidence that *Sterechinus* receives increasing trophic support from diatoms in higher ice cover areas to the south (Fig. 4, Table 3). *Sterechinus* is a generalist feeder that consumes macroalgae, microalgae, seal feces, diverse invertebrates, and carrion (Brand 1980, McClintock 1994). *Sterechinus* was more abundant at our southern study sites relative to the northern sites (Amsler et al. 2023). Even though *Sterechinus* is a mobile consumer (the only mobile consumer to have significant DISTLM results), it is strongly affected by ice cover like the sessile consumers, perhaps because it is more closely reliant upon basal production by seaweeds for food (Norkko et al. 2007) and is known to exhibit large seasonal variation in its energy uptake (Brockington et al. 2001). Its food is dominated by the macroalgae *Desmarestia* spp. year-round (probably dead individuals) but with increased use of other heterotrophs such as bryozoans in winter (Brand 1980). The total bacteria-derived fatty acids in *Sterechinus* decreased with increasing ice cover. The hypothesis that its fatty acids are connected to algal availability is supported by both multivariate and univariate fatty acids analyses; there is a large distance of the urchin from the other related echinoderms in the nMDS (Fig. 3). Thus, it is likely that this sea urchin is tied more closely to macroalgal resources in areas where those are abundant (low ice cover) and diatoms in areas where the benthic production is not dominated by seaweeds (high ice cover). The diatom marker 16:1 ω 7 had a positive relationship with ice cover in *Sterechinus*, providing strong evidence that non-macroalgal production from diatoms (whether they originated in benthic, pelagic, or ice-associated habitats), is an important food in areas with lower macroalgal abundance. Therefore, the ice gradient, which strongly

drives algal abundance, likely impacts the trophic ecology of *Sterechinus*, even though it can move around at small scales to search for food.

The fatty acid signatures of the gastropod *Nacella* did not differ among sites or across the ice cover gradient and large spatial seaweed ecotone. *Nacella* was the consumer with the lowest percentage of variation explained by the ice cover gradient analysis. *Nacella* is a generalist consumer that feeds primarily on benthic diatoms (when abundant in the austral spring and summer), microbial films, microphytobenthos, calcareous algae, seaweeds, bryozoans, and sessile invertebrates (Brand 1980, Suda et al. 2015). Using stable isotopes, Choy et al. (2011) identified that *Nacella* on King George Island (in the northern AP region) is flexible in its resource use across a gradient of habitats, emphasizing microphytobenthos and macroalgal-derived resource assimilation. The fact that the fatty acid signatures of *Nacella* did not change consistently across our sites that varied largely in their macroalgal abundance, lends support to the hypothesis that they focus on calcareous algae, diatoms, and biofilms, or opportunistically scavenge on non-macroalgal resources, such as invertebrates, across the western AP. Evidence supporting this hypothesis includes the position of *Nacella* in the nMDS (Fig. 3), associated with the red algae and diatoms. However, while MUFAs of *Nacella* increased with ice cover, the diatom-specific biomarker 16:1 ω 7 did not increase, suggesting that red algae, rather than diatoms, are driving this pattern and may be an important trophic resource for this grazer at higher levels of ice cover. Intertidal *Nacella* in King George Island had differences in specific fatty acids because of increased stress associated with its shell-encrusting epibiotic coralline algae (Cho et al. 2022). The amount of encrusting coralline red algae did not change across the ice cover gradient studied here (Amsler et al. 2023, their Fig. 7); however, we did not sample coralline algae for fatty acid analysis in our project, and are limited in our ability to interpret the role of this resource in the consumers. Despite the wide range in algal and invertebrate cover among study sites, there is no clear evidence of nutritional stress based on fatty acids in our study, even though many of the consumers studied here are known predators of *Nacella*, including *Neosmilaster* (Mahon et al. 2002), *Perknaster*, *Odontaster*, and even *Sterechinus* (reviewed by Suda et al. 2015).

Ice cover was a significant explanatory variable in DISTLM analysis of the fatty acid signatures of the sea stars *Neosmilaster* and *Perknaster* and was highly significant in *Odontaster*. However, the DISTLM did

not explain a large amount of the total variation in any of the sea stars, including *Odontaster*, so this result is interpreted with caution. All 3 sea stars are known to be relatively mobile scavenging, necrophagous, and predatory consumers (McClintock 1994), and are therefore expected to forage at a higher trophic level, on a higher diversity of prey than other taxa that target basal producers. Because the relative composition of sessile invertebrate spaceholders varied across our study sites, the fatty acid signatures of predators might even be expected to change across this gradient if their diets are a function of the available prey. *Odontaster* was the only sea star for which the key univariate fatty acid categories varied across the ice gradient; MUFAs increased and PUFAs decreased with ice cover. *Odontaster* is also known to consume detrital algal resources (McClintock 1994) and sponges (Dayton et al. 1974). Across the ice gradient, fatty acids of *Odontaster* declined in PUFAs (which were consistently high in seaweeds), possibly as a result of decreased availability of seaweeds, and showed increases in MUFAs, tracking the patterns of the sponge *Dendrilla*. *Perknaster fuscus* is a known predator of sponges in McMurdo Sound (Dayton et al. 1974); *P. aurorae* studied here may likewise prey upon sponges. *Perknaster* did show a slight but statistically significant increase in total 16:1 ω 7 with lower ice cover, which was an important biomarker in the content of the sponge *Dendrilla* (Figs. 3 & 4).

Due to the large geographical range of sites sampled, and the observed variation in fleshy macroalgal cover across the study sites of the present study, we expected to find differences in the nutritionally important PUFAs in the seaweeds and consumers, which are supported by these resources. However, there were no consistent ecosystem-level changes in the nutritionally important PUFAs or any specific fatty acid or summary variable that transcended across all taxa. MUFAs did differ across the ice gradient for 5 of the 8 consumers, but the directionality of the relationship was not consistent, and the affected consumers were from different modalities and phyla. Taken together, the fatty acid signature results indicate that sessile or slow-moving invertebrate consumers, which cannot move to forage for diverse resources, are more likely to be negatively affected trophically by a future with less ice cover on the western AP. While all consumers that we focused on in the present study were collected from at least 9 rocky subtidal sites across the sea ice gradient, this does not imply that they are equally distributed in terms of abundance or biomass. Given the limitations of our bottom time during SCUBA dives and the method of sampling we car-

ried out to describe these patterns, we were not able to quantify biomass or density for most organisms. Future work will be needed to assess the relationships between observed percent cover and species-specific biomass conversions.

A common theme when discussing the dominant feeding modes or trophic guilds of most marine consumers is that nearly all organisms can actually be most accurately classified as 'omnivores', particularly in food webs that receive significant spatial subsidies of nutrients (Polis & Strong 1996). This phenomenon is common in the food webs of the open ocean, due to prey switching, incorporation of particulate organic carbon derived from many sources, or ontogenetic changes in diet through time (e.g. larval heterotrophs in the plankton may focus on phytoplankton early in life and switch to predation later in life) (Isaacs 1977, Landry 1981), but these issues also apply to benthic food webs. The existing literature on the trophic ecology of the Antarctic benthos is rich with observations of a wide diversity of prey consumption by all of the taxa investigated here (Dayton et al. 1974, Brand 1980, McClintock 1994, Amsler et al. 1999, Gili et al. 2001, Tatián et al. 2008, Suda et al. 2015). Variability in energy pathways through Antarctic benthic food webs (e.g. producer-based or detritus-based) that include overlapping species within the same bay can be established based on site-level differences (soft sediment or rocky substrates) (Cordone et al. 2020). In our discussion of each consumer's trophic ecology, we have therefore not attempted to pin each consumer into a place on a theoretical hierarchical pyramid of distinct trophic levels, but rather have focused on their resource assimilation in the context of their modality (i.e. sessile or mobile). The fatty acid signature approach used here to infer trophic ecology inherently embraces this uncertainty since the fatty acid composition of a consumer is a time-integrated reflection of not only snapshots of the diets consumed, but of what is ultimately incorporated into the tissues of the consumer (Graeve et al. 1994, Budge et al. 2006, Galloway & Budge 2020).

In the large body of literature investigating how climate change is affecting marine net primary productivity (NPP), algal standing stock, and its ecosystem consequences, there is a general bias in research effort toward studies on production by marine phytoplankton and the sea ice-associated microbial community (e.g. Wing et al. 2018) rather than seaweeds. This bias is understandable, considering that at the global scale, macroalgae are thought to contribute only about ~3% or $1.32 \text{ Pg C yr}^{-1}$ of global annual marine NPP (Duarte et al. 2022), whereas phytoplank-

ton NPP is $\sim 47 \text{ Pg C yr}^{-1}$ (Field et al. 1998). However, macroalgal productivity is relatively more important in nearshore areas, e.g. representing between ~20% of NPP (Duarte et al. 2022) or up to 10 times the total NPP (Pessarrodona et al. 2022) of coastal phytoplankton. Ultimately, the sensitivity of the dynamics of nearshore primary and secondary production driven by macroalgae in response to climate change is less well understood. Very little is known about how large-scale changes to sea ice will impact macroalgae and what consequences this will have on the food webs of Antarctica (Dunton 2001, Cardona et al. 2021, Iken et al. 2023, Amsler et al. 2023), and no studies to date have approached the questions in this study system at a large geographic scale using fatty acids as trophic biomarkers. Because of this knowledge gap, the research herein focused on the biomarkers of benthic macroalgal producers; however, it is expected that future reduction in sea ice cover in Antarctica will also affect macroinvertebrates, which rely on energy derived from the sea ice microbial community (Wing et al. 2018). Future work along the changing ice cover gradients of Antarctica should attempt to differentiate consumer assimilation of carbon from multiple sources of production, including ice-associated microbes, pelagic phytoplankton, and macroalgae.

The research herein focused on interpretation of the trophic ecology of producers and invertebrate consumers across a large geographical range of sites that experience multiple differences in their environment. Yet, our focus was on interpreting the findings in the context of only ice cover, which is just one key factor that can affect benthic food webs. Other factors that were not evaluated quantitatively here include physical variables such as sea surface temperature, turbidity, irradiance, depth, disturbance from ice-scour, and biological drivers such as pelagic chlorophyll concentration and ice-associated microbial biomass. It should be noted, however, that in the case of turbidity, while it was not measured at the time of sampling, we constrained site selection within a window of consistent satellite-determined turbidity at each study site, in advance (Amsler et al. 2023). There were real limitations to the data we could collect from these remote study sites, during one cruise, where no long-term instruments were deployed for measuring these other variables. The samplings of the biological communities at each location are a snapshot in time; thus, even the limited chlorophyll and temperature data we observed at the time of the field work would not be useful for interpreting trophic biomarkers that are integrated into the tissues of organisms over the

scale of months. Because of the limitations, our research was based on testing the *a priori* hypothesis that sea ice cover (which reduces light penetration to the seafloor) would be a significant factor driving macroalgal abundance across these study sites (Amsler et al. 2023). While we acknowledge that other factors are likely important, annual sea ice alone explained 79% of the total variation in fleshy macroalgal cover at our study sites (Amsler et al. 2023), making this a very good singular satellite-derived proxy for understanding this system. Fatty acid signatures of heterotrophs represent the time-integrated assimilation of prey, and because tissue turnover times are likely very slow, but are still presently unknown for all of the consumers included in this study, we are not able to interpret the results in the context of season or time. Future work should evaluate the seasonal and inter-annual variability of consumers in fixed locations.

5. CONCLUSIONS

Our results suggest that expected future changes to annual ice cover along the western AP (Amsler et al. 2023), are more likely to affect sessile consumers, even if they are from diverse taxonomic groups and feeding modes. Benthic consumers with varied feeding strategies receive significant resource subsidies to their secondary production from seaweeds in polar food webs (Renaud et al. 2015, Michel et al. 2019). It is likely that increased algal production on the western AP as a result of declining ice cover will result in both a greater standing stock of fleshy macroalgae and a concurrent rise in detrital subsidies to benthic food webs. An increased degree of resource subsidization (Polis et al. 1997) in a system is expected to confer increased stability of food webs (Huxel et al. 2002). We found that the fatty acids of most sea stars, which are mobile scavengers and predators, and the mobile ubiquitous limpet *Nacella*, often considered to be a grazer of biofilms, were not consistently sensitive to the sea ice cover gradient and are, therefore, relatively less likely to be trophically impacted by future changes in ice cover that is expected for this region. The summary fatty acids and multivariate fatty acid signatures of the seaweeds were not particularly sensitive to the ice cover gradient. This implies that while seaweeds are poised to increase in biomass and benefit from decreases in ice cover along the western AP, the most dominant and widely distributed fleshy macroalgae will not likely change significantly in their fatty acids, a key indicator of nutritional value.

Acknowledgements. The funding for this work was provided by the National Science Foundation awards to A.W.E.G. (ANT-1744570), K.I. (ANT-1744602), A.G.K. (ANT-1744584), and to C.D.A. and J.B.M. (ANT-1744550). We gratefully acknowledge the Captain and crew of the ARSV 'Lawrence M. Gould' and the Antarctic Support Contract staff. We thank Mike Thomas, Natalie Thomson, and Reyn Yoshioka for assistance in the lab.

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*Editorial responsibility: Eric Sanford,
Bodega Bay, California, USA
Reviewed by: A.F. Ziegler and 2 anonymous referees*

*Submitted: August 22, 2023
Accepted: March 21, 2024
Proofs received from author(s): April 30, 2024*