



Seasonal and ocean basin-scale assessment of amino acid $\delta^{15}\text{N}$ trends in a Southern Ocean marine predator

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ABSTRACT: The Southern Ocean exhibits substantial spatio-temporal variation in biogeochemical processes that shape interactions and productivity across food webs. Stable isotopes in marine predators provide an opportunity to capture such variations, yet few studies have accounted for variability in the isotopic baseline when interpreting predator isotope values. Using bulk $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and the $\delta^{15}\text{N}$ values of amino acids (AAs) of blood from female Antarctic fur seals (AFSs) *Arctocephalus gazella*, we investigated spatial and seasonal variation in baseline $\delta^{15}\text{N}$ ($\delta^{15}\text{N}_{\text{baseline}}$) values across 3 Southern Ocean basins (Indian, Pacific and Atlantic) to facilitate robust comparison of consumer trophic ecology. We detected spatial and seasonal differences in $\delta^{15}\text{N}_{\text{baseline}}$ values across the basins, using the source AAs phenylalanine (Phe) and lysine (Lys), consistent with the latitudinal gradient of AFS colonies and seasonal changes in seal foraging movement. The $\delta^{15}\text{N}$ values of source AAs from Marion Island and Cape Shirreff were representative of particulate organic matter $\delta^{15}\text{N}$ values in the Indian and southwest Atlantic sector, respectively, whereas more complex patterns were observed in the Atlantic sector around Bird Island. Variations in bulk $\delta^{15}\text{N}$ values can also be attributed to changes in AFS diet, with females foraging in the Atlantic and Pacific targeting higher trophic level prey in winter. Trophic position estimation using Phe and leucine (Leu) suggested that females encompass more than 2 trophic levels. Our study highlights the utility of using Lys alongside Phe to assess seasonal and ocean basin-level variations in the isotopic baseline and Leu/Phe for AFS trophic position estimation.

KEY WORDS: Compound-specific isotope analysis · Trophic position · Nitrogen · Southern Ocean · Antarctic fur seal · *Arctocephalus gazella* · Isotopic baselines

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1. INTRODUCTION

Marine ecosystems are inherently spatially and temporally complex. Accounting for these dynamics is crucial for understanding their functioning and to inform effective resource management in the context of rapid anthropogenic climate change (Pecl et al. 2017, Cavanagh et al. 2021). From the tropics to the poles, variations in physical (e.g. temperature, currents, fronts, sea ice cover; Sokolov & Rintoul 2009, Abraham et al. 2013, Moore et al. 2013) and chemical (e.g. oxygen, nutrient availability; Somes et al. 2010, Moore et al. 2013, Breitburg et al. 2018) processes create distinct oceanographic conditions. These conditions support a wide array of open pelagic and coastal marine ecosystems characterized by specific compositions and abundances of species and unique food web structures (Crowder & Norse 2008, Constable et al. 2014, Poloczanska et al. 2016). Seasonality plays an important role in shaping the networks of interactions among species that underpin these ecosystems by driving fluctuations in productivity and resource availability, which can propagate through the entire food web, from microbes to top predators (Constable 2003, Asch 2019). The Southern Ocean holds particular importance in this context, as it is one of the most highly seasonally productive environments globally (Sarmiento et al. 2004), and variation in the physical and chemical environment influences variation in food web structure at multiple scales (Constable 2003, De Broyer et al. 2014, McCormack et al. 2021). Approaches that consider variation across biogeographic regions and seasons are particularly important to provide a comprehensive view of the structural and functional complexity of Southern Ocean marine ecosystems at particular spatiotemporal scales. However, such integrative approaches are deficient for the Southern Ocean, because of constraints on data availability (Bonnet-Lebrun et al. 2023).

Within this context, marine predators serve as valuable indicators to better understand ecosystem functioning and for monitoring ecosystem responses to changes in the marine environment (Carpenter-Kling et al. 2019, Hazen et al. 2019, Bestley et al. 2020). Through their ability to integrate trophic information from the bottom to the top of the food web, higher trophic level predators can be used to assess energy flow and baseline productivity underpinning food webs (Pethybridge et al. 2018a, Seyboth et al. 2018, MacKenzie et al. 2019, Carpenter-Kling et al. 2020, de la Vega et al. 2022). Using retrospective biogeochemical techniques, such as stable isotope analysis, it is feasible to study trophodynamics through wide-rang-

ing predators that migrate across broad geographic regions and through seasons (Trueman et al. 2012, Trueman & St John Glew 2019, Walters et al. 2020). Two of the most used isotopes are $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measured in consumer protein that can be matched to an isotope gradient across the animal's foraging range (McMahon et al. 2013, Trueman & St John Glew 2019). Consumer proteins are enriched in ^{15}N relative to the proteins of their prey in a predictable manner (DeNiro & Epstein 1981). Consequently, $\delta^{15}\text{N}$ provides an indicator of consumer trophic position (TP) and nitrogen sources fueling the food web (Post 2002). In contrast, $\delta^{13}\text{C}$ only slightly increases along the food web and is thus commonly used to trace the origin of the production supporting the food web (Kelly 2000).

However, interpreting tissue bulk isotope compositions at higher trophic levels is challenging due to various factors, particularly the spatial and temporal variability in the isotopic baseline, making it difficult to determine the causes of observed variations in predator tissues (Boecklen et al. 2011). Significant spatiotemporal variability in $\delta^{15}\text{N}$ values in primary producers (e.g. phytoplankton), consumers and particulate organic matter have been observed across the global oceans, including the Southern Ocean (Jennings & Warr 2003, Somes et al. 2010, Espinasse et al. 2019, St John Glew et al. 2021). Variations in $\delta^{15}\text{N}$ values in primary producers can be influenced by community composition, nutrient sources (e.g. nitrate, nitrite, ammonium), nutrient pool size and isotopic fractionation during nitrogen fixation, uptake, assimilation, nitrification and denitrification processes (Somes et al. 2010, Sigman & Fripiat 2019). The $\delta^{15}\text{N}$ values in phytoplankton tend to be higher in productivity hot spots like upwelling regions around coastlines and lower in pelagic oceans (i.e. areas of nitrogen fixation; Somes et al. 2010). In the Southern Ocean, there is a poleward decrease in phytoplankton $\delta^{15}\text{N}$ values, along with variations between basins and across seasons (DiFiore et al. 2010, Espinasse et al. 2019, St John Glew et al. 2021). These spatial $\delta^{15}\text{N}$ gradients at the base of the food web are still discernible in higher trophic levels, allowing the study of predator trophic ecology across varying temporal and spatial scales (Graham et al. 2010, McMahon et al. 2013, Pethybridge et al. 2018a, McMahon & Newsome 2019).

Compound-specific isotope analysis of amino acids (CSIA-AA) is a valuable tool that facilitates better identification of trophic effects due to the integration of underlying variation in primary production sources (Chikaraishi et al. 2009, McMahon & Newsome 2019, Magozzi et al. 2021). The $\delta^{15}\text{N}$ values of amino acids ($\delta^{15}\text{N}_{\text{AA}}$) provide information about the 'source' amino

acids (e.g. phenylalanine), which are directly routed from the prey into the predator tissues, reflecting the $\delta^{15}\text{N}$ values of primary producers, and 'trophic' amino acids (e.g. glutamic acid), which undergo transformations during assimilation, showing stepwise enrichments with each trophic level (McClelland & Montoya 2002, Chikaraishi et al. 2007, 2009, Popp et al. 2007, McMahon & McCarthy 2016, McMahon & Newsome 2019). This approach provides information about the trophic position of a consumer while accounting for the nitrogen isotopic value at the base of the food web, using a single organism (Chikaraishi et al. 2009, Nielsen et al. 2015, McMahon & McCarthy 2016). Analysing bulk $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_{\text{bulk}}$) and $\delta^{15}\text{N}$ ($\delta^{15}\text{N}_{\text{bulk}}$) and $\delta^{15}\text{N}_{\text{AA}}$ values of wide-ranging predators can provide a powerful tool to study both trophic structure and nitrogen sources supporting production within and across ecosystems (Pethybridge et al. 2018b, McMahon & Newsome 2019). Several studies have validated this approach to infer the migration patterns and trophic ecology of marine predators (Ruiz-Cooley et al. 2014, Lorrain et al. 2015, Feddern et al. 2022, Rita et al. 2024) and to detect temporal environmental changes (de la Vega et al. 2022, 2023). In the Southern Ocean, only a limited number of studies have successfully incorporated spatial variations in the isotopic baseline when interpreting predator isotope values (Lorrain et al. 2009, Brault et al. 2019, Lübcker et al. 2021) and none, to our knowledge, has incorporated seasonal variation. Here, we investigated seasonal variation in baseline $\delta^{15}\text{N}$ ($\delta^{15}\text{N}_{\text{baseline}}$) values across 3 ocean basins (Indian, Pacific and Atlantic sectors of the Southern Ocean) using $\delta^{15}\text{N}_{\text{AA}}$ values of a highly mobile, circumpolar species, the female Antarctic fur seal (AFS) *Arctocephalus gazella* to facilitate robust comparisons of consumer trophic ecology.

The AFS is an important and numerous Southern Ocean predator, with breeding colonies located from various sub-Antarctic islands to the northern tip of the Antarctic Peninsula (Forcada & Staniland 2009, Roper-Coudert et al. 2014). The diet of females varies with the location of the colony due to differences in the local conditions and the availability and accessibility of prey species, notably due to the large latitudinal gradient in breeding range. For Bird Island and Cape Shirreff colonies in the Atlantic sector, which encompass the core southern distribution of the species, their summer diet contains a high proportion of Antarctic krill *Euphausia superba*, followed by fish and cephalopods (Reid & Arnould 1996, Casaux et al. 2003, 2016, Osman et al. 2004, Harrington et al. 2017, Abreu et al. 2019). In contrast, females predominantly feed on myctophid fishes and squid at colonies in the Indian

sector (such as Marion Island) located at the northern edge of their breeding range, and further north of the Polar Front (PF) where Antarctic krill does not occur (Klages & Bester 1998, Makhado et al. 2008, Reisinger et al. 2018). However, those studies analysed scat and stomach contents, focusing primarily on the breeding period, when female AFS are accessible as they forage close to their colonies to regularly provide milk to their pups. During the inter-breeding period (May–November), female AFSs occupy a greater geographical range (sub-Antarctic to Antarctic zones, SAZ and AZ, respectively) due to long-distance movements (Guinet et al. 2001, Bailleul et al. 2005, Arthur et al. 2017). Recent bulk stable isotope analyses have provided additional insight into the trophic ecology of female AFSs (Tarrowx et al. 2016, Jones et al. 2020, Walters et al. 2020); however, none of these studies incorporated variations in the isotopic baseline when interpreting AFS isotope values. Understanding food web baseline dynamics and changes in the seal trophic ecology is essential, especially given the overlap with intensified krill fishing activities and the recent documented changes in AFS populations in the Atlantic sector (Forcada et al. 2023, Krause et al. 2024).

Here, we combined $\delta^{13}\text{C}_{\text{bulk}}$ and $\delta^{15}\text{N}_{\text{bulk}}$ values and $\delta^{15}\text{N}_{\text{AA}}$ values of whole blood collected from adult female AFSs from breeding sites in the southern Indian and Atlantic sectors during the pre- and post-breeding periods. We focus on 2 key questions: (1) What is the seasonal and spatial variation in $\delta^{15}\text{N}_{\text{baseline}}$ across the 3 Southern Ocean basins? (2) How do these baseline variations influence the trophic ecology of female AFSs, using trophic amino acid $\delta^{15}\text{N}$ values and trophic position (TP) estimations? This approach will enhance our understanding of the spatiotemporal patterns in the Southern Ocean food webs on which these seals depend. We hypothesized significant spatial variations in the isotopic baseline, with strong differences expected in summer, when female AFSs forage in localised areas around their colonies. Specifically, we expected higher $\delta^{15}\text{N}_{\text{baseline}}$ values for females from Marion Island foraging in the SAZ compared to those from Bird Island and Cape Shirreff (Table 1). In contrast, we expected reduced spatial variation in the isotopic baseline in winter, when female seals exhibit wide-ranging foraging behaviour, thus integrating isotopic information across various food web baselines. Furthermore, we predicted spatial variation in AFS trophic ecology, particularly in summer, when dietary preferences diverge significantly between colonies and there is marked seasonal variation in trophic ecology of the females within each colony, due to long-distance movements of females during the winter period.

Table 1. Foraging ecology of female Antarctic fur seals *Arctocephalus gazella* during the breeding and non-breeding periods at Bird Island, Cape Shirreff and Marion Island

Breeding site	Foraging habitat		Diet		References
	Breeding season	Non-breeding season	Breeding season	Non-breeding season	
Marion Island	Sub-Antarctic Zone Open ocean	Sub-Antarctic Zone Polar Frontal Zone Antarctic Zone Open ocean	Myctophids Cephalopods	Myctophids Cephalopods Krill spp.	Klages et al. (1998), Makhado et al. (2008), Arthur et al. (2017), Reisinger et al. (2018), Wege et al. (2019), Walters et al. (2020)
Bird Island	Antarctic Zone Open ocean	Sub-Antarctic Zone Polar Frontal Zone Antarctic Zone Open ocean Patagonian Shelf	Antarctic krill Myctophids Nototheniids	Antarctic krill Myctophids Nototheniids Cephalopods	Brown et al. (1999), Boyd et al. (2002), Staniland et al. (2010), Waluda et al. (2010), Arthur et al. (2017), Jones et al. (2020), Walters et al. (2020)
Cape Shirreff	Southern Zone Sea ice zone	Sub-Antarctic Zone Polar Frontal Zone Antarctic Zone Southern Zone Open ocean	Antarctic krill Fish	Fish Cephalopods Antarctic krill	Polito & Goebel (2010), Arthur et al. (2017), Hinke et al. (2017), Borrás-Chávez (2020), Walters et al. (2020)

2. MATERIALS AND METHODS

2.1. Study sites and sample collection

Whole blood samples were collected from female AFSs breeding at 3 circumpolar sites in the Southern Ocean: (1) Marion Island (46° 52' S, 37° 51' E), in the Indian sector, (2) Bird Island (54° 00' S, 38° 02' W), off the northwest tip of South Georgia in the southwest Atlantic sector and (3) Cape Shirreff (62° 28' S, 60° 48' W), on the north coast of Livingston Island, in the South Shetland Islands, near the tip of the Antarctic Peninsula on the edge of the Pacific sector (Fig. 1). These 3 colonies encompass a large latitudinal and longitudinal range. Marion Island is located in the SAZ, between the sub-Antarctic Front (SAF) and the PF (Treasure et al. 2015); Bird Island lies in the AZ, between the PF and the Southern Antarctic Circumpolar Current Front (SACCF), while Cape Shirreff is located within the seasonal ice zone south of the Southern Boundary Front (Fig. 1; Park et al. 2019). The 3 colonies are part of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) convention areas: Sub-area 48.1 for Cape Shirreff, 48.3 for Bird Island and 58.7 for Marion Island. The AFS is a key indicator species for resource management in the Southern Ocean ecosystem within the CCAMLR framework. In particular, the CCAMLR Ecosystem Monitoring Program (CEMP) designates Bird Island and Cape Shirreff as crucial

monitoring sites for AFS, emphasizing their importance in tracking ecosystem changes and informing sustainable management practices for harvested species like Antarctic krill.

Whole blood samples (1–5 ml) were collected from a hind flipper interdigital vein from adult female AFSs in 2008, 2009 and 2010 (n = 127) (Table S1). Blood was sampled as soon as possible after females arrived at the breeding colony (mean ± SD, Bird Island: 9.07 ± 11.5 d after arrival; Cape Shirreff: 5.5 ± 8.8 d after arrival; Marion Island: 10.2 ± 9.6 d after arrival), and again at the end of the breeding season. Whole blood provides an indication of the consumer trophic ecology over the past 2–3 mo (Hilderbrand et al. 1996, Vander Zanden et al. 2015). Samples collected at the start of the breeding season thus represent the last few months of the inter-breeding period, while samples collected at the end of the breeding season reflect foraging during the summer breeding period.

2.2. Stable isotope analysis

Samples were stored at –20°C until isotopic analysis. Blood samples were dried at 60°C for at least 24 h prior to bulk and compound-specific stable isotope analyses (Walters et al. 2020). Dried blood samples were analysed for bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($\delta^{13}\text{C}_{\text{bulk}}$ and $\delta^{15}\text{N}_{\text{bulk}}$) by combusting them in a Carlo-Erba EA1100 (CE Instruments) and passing

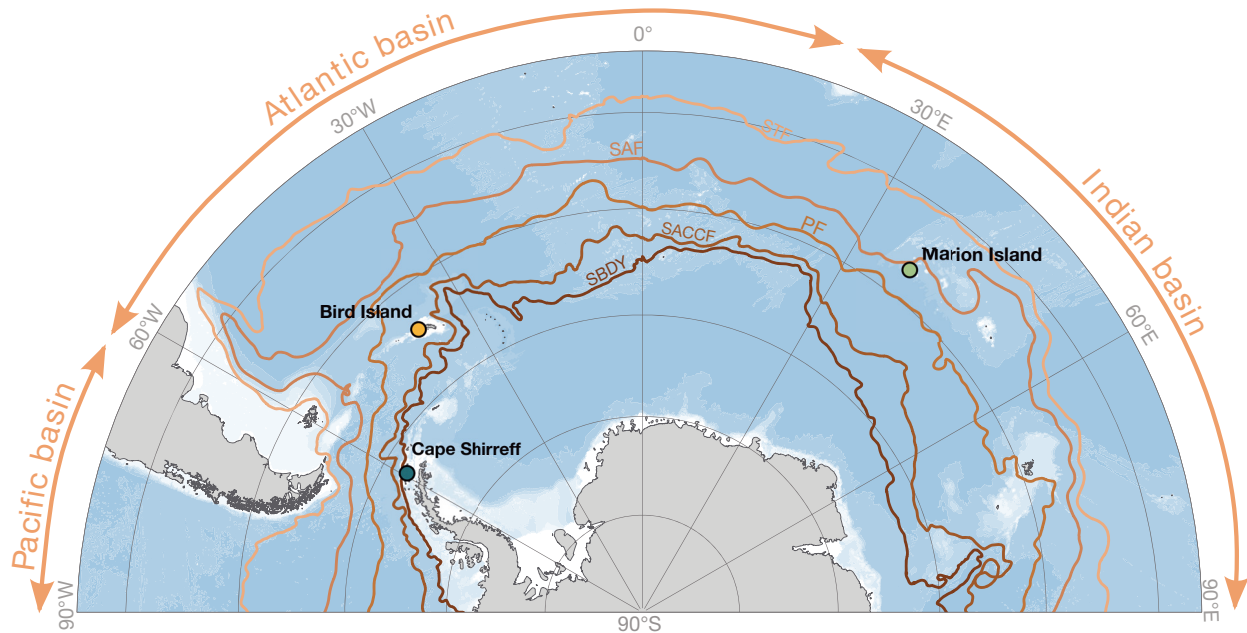


Fig. 1. Locations where female Antarctic fur seal blood samples were collected in the Atlantic and Indian sectors of the Southern Ocean. Samples were collected during the summer and winter seasons in 2008, 2009 and 2010. Coloured lines indicate mean frontal position (Park et al. 2019), from lighter to darker colour: STF: Sub-tropical Front; SAF: Sub-Antarctic Front; PF: Polar Front; SACCF: Southern Antarctic Circumpolar Current Front; SBDY: Southern Boundary of the Antarctic Circumpolar Current

the separated gases produced to an Isoprime (Elementar) continuous-flow isotope ratio mass spectrometer (IRMS). All samples were processed at the Farquhar Laboratory, Australian National University (ANU), Canberra. Replicate measurements of internal laboratory standards for $\delta^{15}\text{N}$ (glycine, cysteine) and $\delta^{13}\text{C}$ (glycine, cane sugar and beet sugar) indicated internal precisions better than 0.15‰, for both. Internal standards were previously calibrated against interlaboratory comparison standards distributed by the International Atomic Energy Agency (IAEA) and the USGS (L-glutamic acid, USGS 40 and USGS 41), except for ANU cane sugar, which was also the source of IAEA CH-6. Stable isotope ratios were reported using standard δ notation in parts per thousand (‰) deviation from the international standards Vienna PeeDee belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$ as follows:

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

where X is ^{13}C or ^{15}N , and R is the corresponding ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$.

Dried blood samples were analysed for individual amino acid $\delta^{15}\text{N}$ values ($\delta^{15}\text{N}_{\text{AA}}$) using a modified method described by Meekan et al. (2022) at the Commonwealth Scientific and Industrial Research Organisation (CSIRO) laboratories in Hobart, Australia. The modification was the temperature and duration of the initial hydrolysis; we used 20 h at 110°C. The $\delta^{15}\text{N}$

compositions of the individual amino acids were measured with a Trace GC Ultra gas chromatograph coupled to a Delta V Plus IRMS through a GC-C combustion furnace (980°C), reduction furnace (650°C) and liquid N_2 cold trap. Each sample was analysed at least in duplicate. To normalize the $\delta^{15}\text{N}$ values, a set of amino acid standards with known $\delta^{15}\text{N}$ values was used to bracket the 2 distinct IRMS analyses. The slope and intercept of known vs. measured values were then used to correct the measured values for the sample set. The reproducibility of the isotopic analysis of individual amino acids calculated from the bracketing standards was $\pm 0.48\%$ (1 SD) and ranged from ± 0.10 to $\pm 0.71\%$.

Through acid hydrolysis, glutamine (Gln) was converted to glutamic acid (Glu) and asparagine (Asn) was converted into aspartic acid (Asp). As a result, the final measurements combine Gln + Glu (Glx) and Asn + Asp (Asx). Amino acids were categorized into 4 groups: (1) source AAs, lysine (Lys) and phenylalanine (Phe), reflecting $\delta^{15}\text{N}_{\text{baseline}}$ as they are not significantly affected by trophic transfer; (2) trophic AAs, alanine (Ala), valine (Val), Asx, leucine (Leu), proline (Pro) and Glx, which tend to become more enriched in ^{15}N through deamination and transamination as they move up the food web; (3) the metabolic AA threonine (Thr), often involved in transamination, with decreases in values of $\delta^{15}\text{N}$ with each trophic level, leading to negative values; and (4) source/trophic AAs,

glycine (Gly) and serine (Ser), which are challenging to classify, with values often similar within an organism but varying widely between organisms (McMahon & McCarthy 2016, Cherel et al. 2019, Whiteman et al. 2019).

2.3. Data analysis

2.3.1. TP and relative TP (RTP)

Individual TP was calculated using a multi-trophic discrimination factor (TDF) equation and a combination of source and trophic AAs (Germain et al. 2013, McMahon et al. 2019):

$$TP_{Tr-Sr} = [(\delta^{15}N_{Tr} - \delta^{15}N_{Sr} - TDF_2 - \beta) / TDF_1] + 2 \quad (2)$$

where $\delta^{15}N_{Tr}$ and $\delta^{15}N_{Sr}$ represent the nitrogen isotopic values of the trophic and source AAs in the consumer, respectively; TDF_1 represents the trophic discrimination for lower trophic levels, TDF_2 represents the TDF_{Tr-Sr} for higher trophic levels, and β is the difference between the $\delta^{15}N$ values of trophic and source AAs in primary producers (Table S2), taken from Nielsen et al. (2015) and Germain et al. (2013). Borrell et al. (2012) suggested that TDFs remain relatively consistent among taxonomically closely related species, thus we selected the TDF values of the harbour seal *Phoca vitulina* (Germain et al. 2013) due to the absence of a species-specific TDF for AFSs (Text S1). We selected Glx-Phe, as it is the most commonly used amino acid pair in marine predator isotope ecology, and Leu-Phe, which provided the most ecologically realistic TP estimation for AFSs, based on previous dietary information (Table 1, Text S1). Alternative TPs were also calculated using a combination of other trophic (Ala, Asx, Pro, Val) and source (Lys) AAs (Table S3), which gave similar trends in TP between the colonies (Fig. S1). Following the recommendation of Ramirez et al. (2021), propagation of analytical and methodological error was accounted for using the 'propagate' package in R (Spiess 2018), to improve the accuracy of TP estimation.

We also calculated the relative TP (RTP) of each seal (Cherel et al. 2019):

$$RTP = \delta^{15}N_{Tr} - \delta^{15}N_{Sr} \quad (3)$$

expressed in ‰. Contrary to the TP estimation, the RTP does not necessitate *a priori* assumptions about the β and TDF values, thus emphasizing relative differences in food web position (Choy et al. 2015, Cherel et al. 2019).

2.3.2. Statistical analysis

All statistical analyses were performed using R version 4.2.1 (R Core Team 2022). Ocean-basin scale variation in $\delta^{15}N_{bulk}$, $\delta^{13}C_{bulk}$, $\delta^{15}N_{AA}$, TP and RTP within each season were investigated using a linear mixed-effects model with site as a fixed effect and year as a random effect followed by a Tukey's post hoc test to identify significant differences between specific sites. Within-location differences between seasons in $\delta^{15}N_{bulk}$, $\delta^{13}C_{bulk}$, $\delta^{15}N_{AA}$, TP and RTP were examined using another linear mixed-effects model with season as a fixed effect and year as a random effect, followed by a Tukey's post hoc test for pairwise comparisons to test significant differences between seasons. All linear mixed-effects models were fitted using the R package 'lme4'. To determine the general differences in AA compositions between colonies, we performed a multivariate analysis of variance (MANOVA) on $\delta^{15}N_{AA}$ values, considering the interaction effect of site, season and year, followed by a principal component analysis (PCA). We used linear regressions to investigate if variation in $\delta^{15}N_{bulk}$ can be attributed to variation in the isotopic baseline ($\delta^{15}N_{Phe}$, $\delta^{15}N_{Leu}$) and/or trophic effects ($\delta^{15}N_{Glu}$, $\delta^{15}N_{Leu}$).

The $\delta^{15}N$ values of particulate organic matter ($\delta^{15}N_{POM}$) are typically used to represent the food web isotopic baseline (Espinasse et al. 2019). To evaluate if our $\delta^{15}N_{baseline}$ values are representative of the food web isotopic baseline, we compared our $\delta^{15}N_{Phe}$ and $\delta^{15}N_{Lys}$ values to $\delta^{15}N_{POM}$ (Seyboth et al. 2018, Espinasse et al. 2019, Stirnimann et al. 2024) and $\delta^{15}N$ of particulate organic nitrate ($\delta^{15}N_{PON}$) values (only available for the Indian sector; Smith et al. 2022). Values from Cape Shirreff were compared only with Atlantic values in winter, as, to our knowledge, no $\delta^{15}N_{POM}$ values are available for the Pacific sector region.

3. RESULTS

3.1. Blood $\delta^{15}N_{bulk}$ and $\delta^{13}C_{bulk}$ values

The $\delta^{13}C_{bulk}$ and $\delta^{15}N_{bulk}$ values varied between seasons and across the 3 ocean basins (Table 2; Fig. S2 in the Supplement at www.int-res.com/articles/suppl/m747p151_supp.pdf). The $\delta^{15}N_{bulk}$ values at Marion Island were significantly higher than both Cape Shirreff and Bird Island in summer (Tukey HSD, both $p < 0.0001$; Table 2; Table S4). Seasonal comparisons within each colony showed higher $\delta^{15}N_{bulk}$ values in winter for Bird Island (Tukey HSD, $p = 0.034$) and

Table 2. Bulk and individual amino acid $\delta^{15}\text{N}$ values of whole blood from female Antarctic fur seals *Arctocephalus gazella*. Values are means \pm SD. Linear mixed effect modelling followed by Tukey pairwise comparisons was performed to compare bulk and compound-specific stable isotope values, trophic position and relative trophic position between sites or seasons (see Tables S4 & S5 for the models used). Values in the same row with differing superscript letters or signs differ statistically ($p < 0.05$). Superscript letters indicate significant differences between sites within each season (a,b,c for summer; A,B,C for winter), while superscript signs (*, \dagger) show significant differences between seasons within each site

	Bird Island		Cape Shirreff		Marion Island	
	Summer	Winter	Summer	Winter	Summer	Winter
	41	8	12	26	21	19
Blood bulk (%)						
$\delta^{15}\text{N}$	$8.7 \pm 0.7^{a*}$	$9.6 \pm 2.1^\dagger$	$8.8 \pm 0.6^{a*}$	$10.3 \pm 1.0^\dagger$	10.9 ± 0.4^b	10.7 ± 0.7
$\delta^{13}\text{C}$	-20.6 ± 0.8^a	-21.2 ± 1.6	$-23.4 \pm 0.5^{c*}$	$-21.2 \pm 0.9^{A\dagger}$	$-21.4 \pm 0.7^{b*}$	$-22.3 \pm 1.0^{B\dagger}$
Blood amino acid $\delta^{15}\text{N}$ (‰)						
Trophic						
Alanine	$12 \pm 4.8^{a*}$	$17.5 \pm 2.8^\dagger$	$13.4 \pm 4.7^{a*}$	$18.1 \pm 4.5^\dagger$	19.7 ± 3.3^b	19.1 ± 2.9
Valine	$11.5 \pm 3.7^{a*}$	$16.0 \pm 3.1^\dagger$	$14.0 \pm 3.2^{a*}$	$18.1 \pm 3.9^\dagger$	19.0 ± 4.5^b	19.4 ± 2.9
Aspartic acid	$9.7 \pm 3.4^{a*}$	$13.7 \pm 2.5^\dagger$	$11.7 \pm 2.5^{a*}$	$15.4 \pm 2.9^\dagger$	16.3 ± 2.3^b	15.9 ± 1.6
Leucine	$10.2 \pm 4.3^{a*}$	$15.4 \pm 3.1^\dagger$	$13.2 \pm 3.9^{b*}$	$18.1 \pm 4.0^\dagger$	19.4 ± 2.9^c	18.8 ± 2.4
Glutamic acid	$11.8 \pm 4.6^{a*}$	$17.6 \pm 2.6^\dagger$	$14.5 \pm 4.1^{a*}$	$19.0 \pm 4.2^{A\dagger}$	20.0 ± 3.2^b	20.3 ± 2.8
Proline	$9.8 \pm 6.9^{a*}$	$18.8 \pm 3.0^\dagger$	$10.6 \pm 6.5^{a*}$	$18.1 \pm 6.4^\dagger$	20.3 ± 5.6^b	19.4 ± 4.7
Trophic/Source						
Serine	$-0.1 \pm 2.5^*$	$3.9 \pm 3.5^{B\dagger}$	$-1.5 \pm 1.8^*$	$3.7 \pm 2.7^{B\dagger}$	-0.1 ± 2.0	0.6 ± 1.6^A
Glycine	4.3 ± 3.6^a	5.7 ± 1.7	$4.7 \pm 2.8^{a*}$	$6.8 \pm 3.2^\dagger$	8.2 ± 2.3^b	7.6 ± 2.2
Source						
Phenylalanine	-1.8 ± 3.1^a	0.2 ± 1.7	$-1.4 \pm 2.2^*$	$0.3 \pm 3.1^\dagger$	0.6 ± 2.4^b	0.4 ± 1.6
Lysine	$-2.5 \pm 3.5^{a*}$	$1.8 \pm 1.3^{B\dagger}$	$-2.8 \pm 3.0^{a*}$	$0.2 \pm 3.8^{A\dagger}$	-0.1 ± 2.4^b	-0.3 ± 2.4^A
Metabolic						
Threonine	$-23.1 \pm 2.6^{c\dagger}$	$-27.0 \pm 5.0^{B*}$	$-29.0 \pm 3.9^{B\dagger}$	$-33.5 \pm 3.2^{A*}$	$-33.2 \pm 2.6^{A\dagger}$	$-34.5 \pm 3.3^{A*}$
Trophic position						
Glx/Phe	$3.1 \pm 0.3^{a*}$	$3.7 \pm 0.4^{A\dagger}$	$3.5 \pm 0.4^{b*}$	$4.0 \pm 0.3^{A\dagger}$	4.1 ± 0.3^c	4.1 ± 0.3^B
Leu/Phe	$3.6 \pm 0.3^{a*}$	$4.1 \pm 0.4^{A\dagger}$	$4.0 \pm 0.4^{b*}$	$4.6 \pm 0.3^{B\dagger}$	4.8 ± 0.3^c	4.7 ± 0.3^B
Relative trophic position (‰)						
Glx/Phe	$13.6 \pm 1.9^{a*}$	$17.3 \pm 2.3^{A\dagger}$	$15.9 \pm 2.2^{b*}$	$18.7 \pm 1.9^{A\dagger}$	19.4 ± 2.2^c	19.9 ± 2.0^B
Leu/Phe	$12.0 \pm 1.8^{a*}$	$15.2 \pm 2.8^{A\dagger}$	$14.6 \pm 2.0^{b*}$	$17.9 \pm 1.8^{B\dagger}$	18.8 ± 1.6^c	18.4 ± 1.9^B

Cape Shirreff (Tukey HSD, $p < 0.0001$), but no significant differences between seasons for Marion Island females. We did not observe spatial variation in $\delta^{15}\text{N}_{\text{bulk}}$ in winter.

3.2. $\delta^{15}\text{N}_{\text{AA}}$ values

The $\delta^{15}\text{N}_{\text{AA}}$ values of 11 AAs were quantified, including 6 trophic AAs (Ala, Val, Asx, Leu, Glx, Pro), 2 source AAs (Phe, Lys), 2 trophic/source AAs (Ser, Gly) and 1 metabolic AA (Thr). The MANOVA revealed significant differences in $\delta^{15}\text{N}_{\text{AA}}$ values among sites and seasons (Table S5).

The $\delta^{15}\text{N}_{\text{AA}}$ values varied among the 3 colonies and between seasons (Table 2, Fig. 2). The PCA revealed that the trophic AAs, in particular Pro, and the meta-

bolic AA Thr were driving most of the differences among colonies and seasons (Fig. 3). All trophic AAs, the trophic/source AA Gly and the source AA Lys showed significantly higher $\delta^{15}\text{N}$ values in females from Marion Island compared to females from Bird Island and Cape Shirreff in summer (Table 2, Fig. 2; Table S5). Females from Marion Island exhibited significantly higher $\delta^{15}\text{N}_{\text{Phe}}$ values in comparison to females from Bird Island in summer (Tukey's HSD, $p = 0.003$). In contrast, females from Bird Island exhibited higher $\delta^{15}\text{N}_{\text{Lys}}$ values compared to females from Cape Shirreff and Marion Island in winter (Tukey's HSD, $p = 0.019$ and 0.016 , respectively). No differences in $\delta^{15}\text{N}_{\text{Phe}}$ values were detected in winter (Table 2, Fig. 2; Table S5).

The trophic AA Leu and metabolic AA Thr were the only AAs with $\delta^{15}\text{N}$ values significantly different

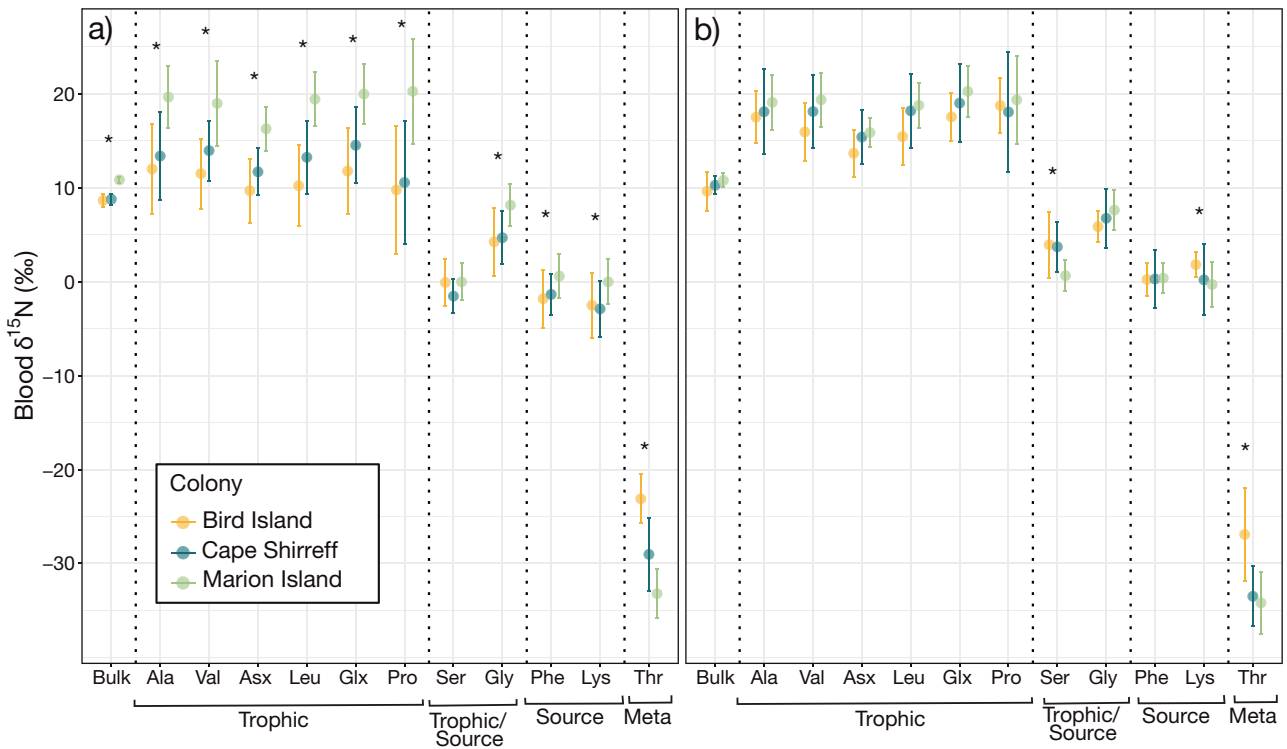


Fig. 2. Mean and SD $\delta^{15}\text{N}$ values of amino acids for adult female Antarctic fur seal *Arctocephalus gazella* whole blood samples from Bird Island, Cape Shirreff and Marion Island during the (a) summer and (b) winter period. Significant differences ($p < 0.05$) in $\delta^{15}\text{N}$ values of amino acid between sites among a season are indicated with asterisks (*). Ala: alanine; Val: valine; Asx: aspartic acid; Leu: leucine; Glx: Glutamic acid; Pro: proline; Ser: serine; Gly: glycine; Phe: phenylalanine; Lys: lysine; Thr: threonine. Amino acids are divided into trophic, trophic/source, source and metabolic (Meta) groups

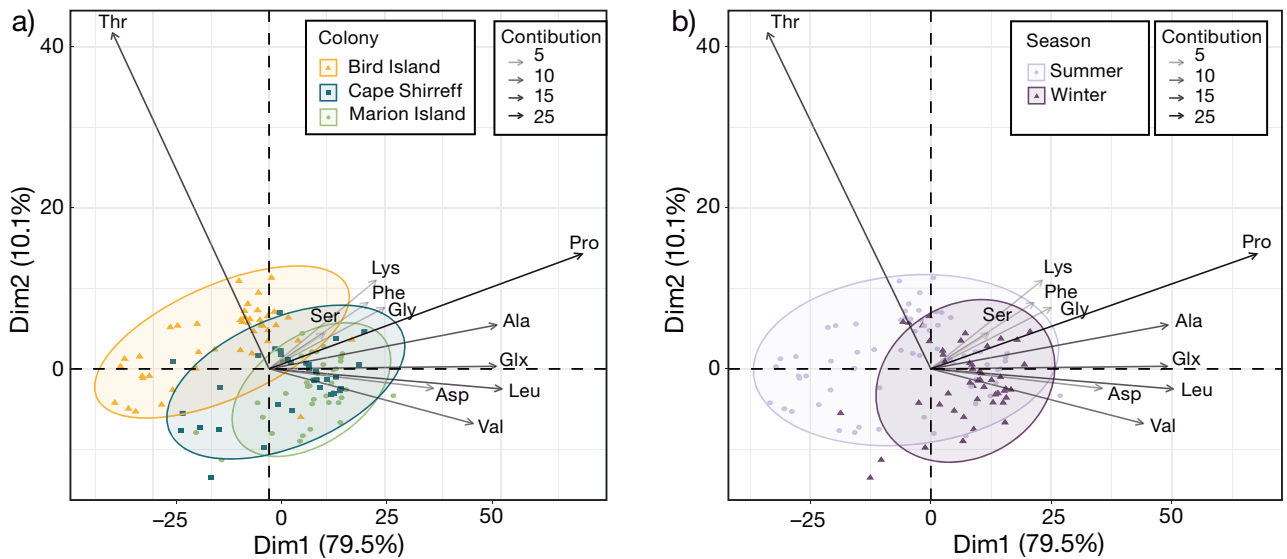


Fig. 3. Principal component analysis of $\delta^{15}\text{N}$ values of amino acids in female Antarctic fur seal *Arctocephalus gazella* whole blood samples from Bird Island, Cape Shirreff and Marion Island (a) among colonies and (b) between seasons. Abbreviations as in Fig. 2

among all 3 colonies in summer (Table 2, Fig. 2; Table S5). Values of $\delta^{15}\text{N}_{\text{Leu}}$ were higher for Marion Island, followed by Cape Shirreff and lower for Bird Island, while Thr showed the opposite trend. In

winter, $\delta^{15}\text{N}$ values of the metabolic AA Thr were higher for Bird Island females compared to those from Cape Shirreff and Marion Island (Tukey's HSD, $p = 0.002$ and <0.0001 , respectively).

Table 3. Comparison of $\delta^{15}\text{N}$ values of source amino acids (phenylalanine and lysine; $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$) from female Antarctic fur seal *Arctocephalus gazella* whole blood and particulate organic matter (POM; $\delta^{15}\text{N}_{\text{POM}}$) from the literature, across 3 foraging zones (Indian, Atlantic and Pacific sector of the Southern Ocean) during summer and winter season. Statistical comparisons between $\delta^{15}\text{N}_{\text{Phe}}$ or $\delta^{15}\text{N}_{\text{Lys}}$ and $\delta^{15}\text{N}_{\text{POM}}$ were conducted using 1-sample *t*-tests; significant differences ($p < 0.05$) are shown in **bold**. †Winter data from Bird Island do not include the 2 individuals foraging over the Patagonian Shelf due to the absence of winter POM data for this area. ‡ Values from Cape Shirreff were compared only with Atlantic values in winter, as no $\delta^{15}\text{N}_{\text{POM}}$ values are available for the Pacific sector region

Colony	Season	Southern Ocean Basin	AFS foraging zone	$\delta^{15}\text{N}_{\text{Phe}}$ (‰)	$\delta^{15}\text{N}_{\text{Lys}}$ (‰)	$\delta^{15}\text{N}_{\text{POM}}$ (‰)	One sample <i>t</i> -test p-values	
							$\delta^{15}\text{N}_{\text{POM}} / \delta^{15}\text{N}_{\text{Phe}}$	$\delta^{15}\text{N}_{\text{POM}} / \delta^{15}\text{N}_{\text{Lys}}$
Marion Island	Summer	Indian	Subantarctic Zone	0.6 ± 2.4	-0.1 ± 2.4	0.9 ± 1.1^a	0.5606	0.09432
	Summer		Subantarctic Zone	0.6 ± 2.4	-0.1 ± 2.4	0.7 ± 0.5^b	0.78	0.1623
	Winter	Indian	Subantarctic Zone	0.4 ± 1.6	-0.3 ± 2.4	-0.5 ± 0.7^b	0.02974	0.7198
			Polar Frontal Zone Antarctic Zone					
Winter	Indian	Subantarctic Zone Polar Frontal Zone Antarctic Zone	0.4 ± 1.6	-0.3 ± 2.4	$-0.3 \pm 1.2^{c,e}$	0.08453	0.9987	
Bird Island	Summer	Atlantic	Antarctic Zone	-1.8 ± 3.1	-2.5 ± 3.5	0.9 ± 1.3^a	<0.0001	<0.0001
	Summer	Atlantic	Antarctic Zone	-1.8 ± 3.1	-2.5 ± 3.5	0.8 ± 0.2^b	<0.0001	<0.0001
	Winter†	Atlantic	Subantarctic Zone Polar Frontal Zone Antarctic Zone	0.20 ± 1.1	1.8 ± 0.70	-0.5 ± 0.7^b	0.1605	<0.001
Cape Shirreff	Summer	Atlantic	Southern Zone	-1.4 ± 2.2	-2.8 ± 3.0	-0.9 ± 1.7^d	0.4783	0.0506
	Winter‡	Atlantic and Pacific	Subantarctic Zone	0.3 ± 3.1	0.2 ± 3.8	-0.5 ± 0.7^b	0.203	0.3681
			Polar Frontal Zone Antarctic Zone Southern Zone					

^aStirnemann et al. (2024); ^bEspinasse et al. (2019); ^cSmith et al. (2022); ^dSeyboth et al. (2018); ^e $\delta^{15}\text{N}$ values from particulate organic nitrogen ($\delta^{15}\text{N}_{\text{PON}}$)

Seasonal variations in $\delta^{15}\text{N}_{\text{AA}}$ values were detected for females from Bird Island and Cape Shirreff. Specifically, $\delta^{15}\text{N}$ values from all trophic AAs, in addition to $\delta^{15}\text{N}_{\text{Ser}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ values, were significantly higher in winter, and $\delta^{15}\text{N}_{\text{Thr}}$ values were higher in summer (Table 2; Table S5). For Cape Shirreff, we also observed a seasonal variation in $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Gly}}$ values, with higher values in winter compared to summer (Tukey's HSD, $p = 0.014$ and 0.019).

During the summer season, $\delta^{15}\text{N}$ values of Phe and Lys were similar to those of $\delta^{15}\text{N}_{\text{POM}}$ at Marion Island and Cape Shirreff, but significantly higher ($p < 0.0001$) than $\delta^{15}\text{N}_{\text{POM}}$ at Bird Island (Table 3). In winter, $\delta^{15}\text{N}$ values of Phe and Lys remained similar to $\delta^{15}\text{N}_{\text{POM}}$ at Marion Island, while $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ values were aligned with $\delta^{15}\text{N}_{\text{POM}}$ at Cape Shirreff. However, at Bird Island, $\delta^{15}\text{N}_{\text{Phe}}$ values were similar to $\delta^{15}\text{N}_{\text{POM}}$, whereas $\delta^{15}\text{N}_{\text{Lys}}$ values were significantly lower (Table 3).

Positive relationships between $\delta^{15}\text{N}_{\text{bulk}}$ values and $\delta^{15}\text{N}_{\text{Phe}}$ ($y = -8.071 + 0.779x$, $r^2 = 0.125$, $p = 0.001$), $\delta^{15}\text{N}_{\text{Glx}}$ ($y = -8.204 + 2.538x$, $r^2 = 0.375$, $p < 0.0001$), $\delta^{15}\text{N}_{\text{Lys}}$ ($y = -9.021 + 0.825x$, $r^2 = 0.098$, $p = 0.001$) and $\delta^{15}\text{N}_{\text{Leu}}$ values ($y = -11.945 + 2.795x$, $r^2 = 0.45$, $p < 0.0001$) were observed (Fig. 4).

3.3. TP and RTP

The estimated TP of females varied from 2.7 to 4.7 for $\text{TP}_{\text{Glx-Phe}}$ and 3.0 to 5.3 for $\text{TP}_{\text{Leu-Phe}}$ (Table 2, Fig. 5; Table S3). Variations in $\text{TP}_{\text{Leu-Phe}}$ among colonies were observed in summer, with females from Marion Island having higher $\text{TP}_{\text{Leu-Phe}}$ than females from Bird Island and Cape Shirreff (Tukey's HSD, both $p < 0.0001$), and females from Cape Shirreff occupying a higher $\text{TP}_{\text{Leu-Phe}}$ compared to females from Bird Island (Tukey's HSD, $p < 0.0001$; Table 2, Fig. 5; Table S4). During the winter, female seals from Marion Island and Cape Shirreff occupied a higher $\text{TP}_{\text{Leu-Phe}}$ compared to females from Bird Island (Tukey's HSD, $p < 0.0001$ and $p = 0.002$, respectively; Table 2, Fig. 5; Table S4), but no difference in $\text{TP}_{\text{Leu-Phe}}$ was detected between females from Marion Island and Cape Shirreff. Within-colony seasonal differences were detected for females from Bird Island and Cape Shirreff, with seals occupying a higher average $\text{TP}_{\text{Leu-Phe}}$ in winter (Tukey's HSD, both $p < 0.0001$; Table 2, Fig. 5; Table S4). A statistically significant positive relationship was detected between $\delta^{15}\text{N}_{\text{bulk}}$ values and

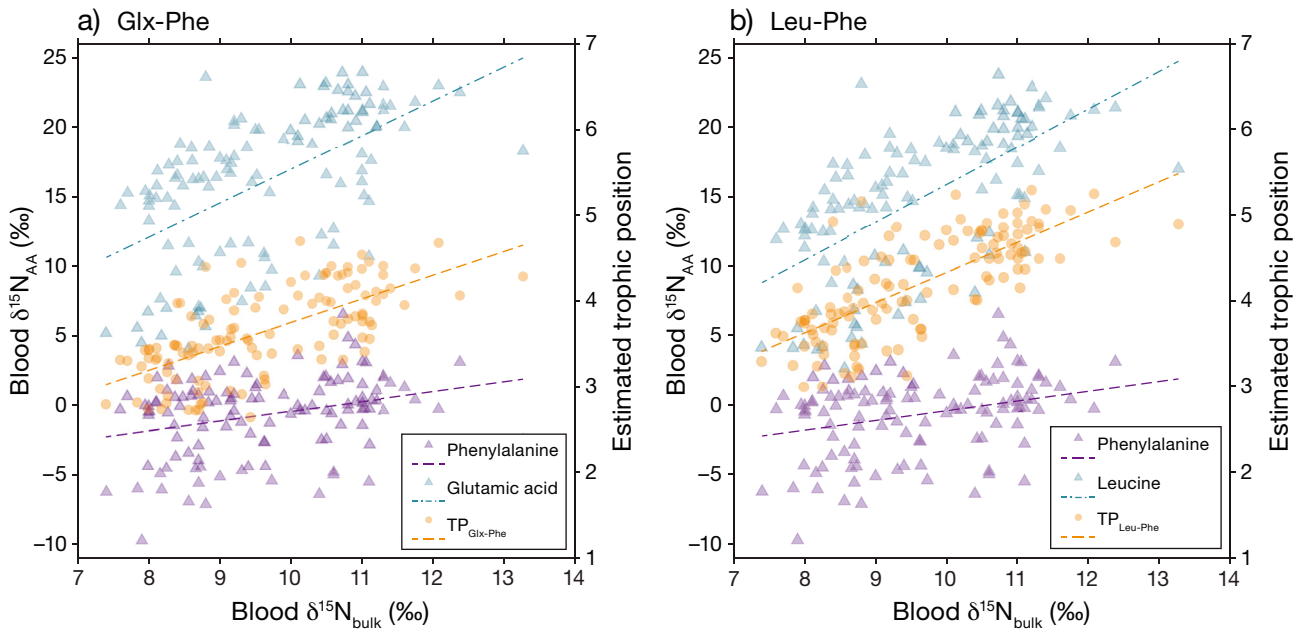


Fig. 4. Bulk $\delta^{15}\text{N}$ values plotted against source (phenylalanine) and trophic (glutamic acid and leucine) amino acids and the derived trophic position obtained from female Antarctic fur seal *Arctocephalus gazella* whole blood. (a) $\delta^{15}\text{N}$ values of phenylalanine ($\delta^{15}\text{N}_{\text{Phe}}$), glutamic acid ($\delta^{15}\text{N}_{\text{Glx}}$) and their derived trophic position ($\text{TP}_{\text{Glx-Phe}}$); (b) $\delta^{15}\text{N}$ values of phenylalanine ($\delta^{15}\text{N}_{\text{Phe}}$) and leucine ($\delta^{15}\text{N}_{\text{Leu}}$) and their derived trophic position ($\text{TP}_{\text{Leu-Phe}}$). The dotted lines indicate the linear regression between $\delta^{15}\text{N}_{\text{bulk}}$ and $\delta^{15}\text{N}_{\text{AA}}$ or TP

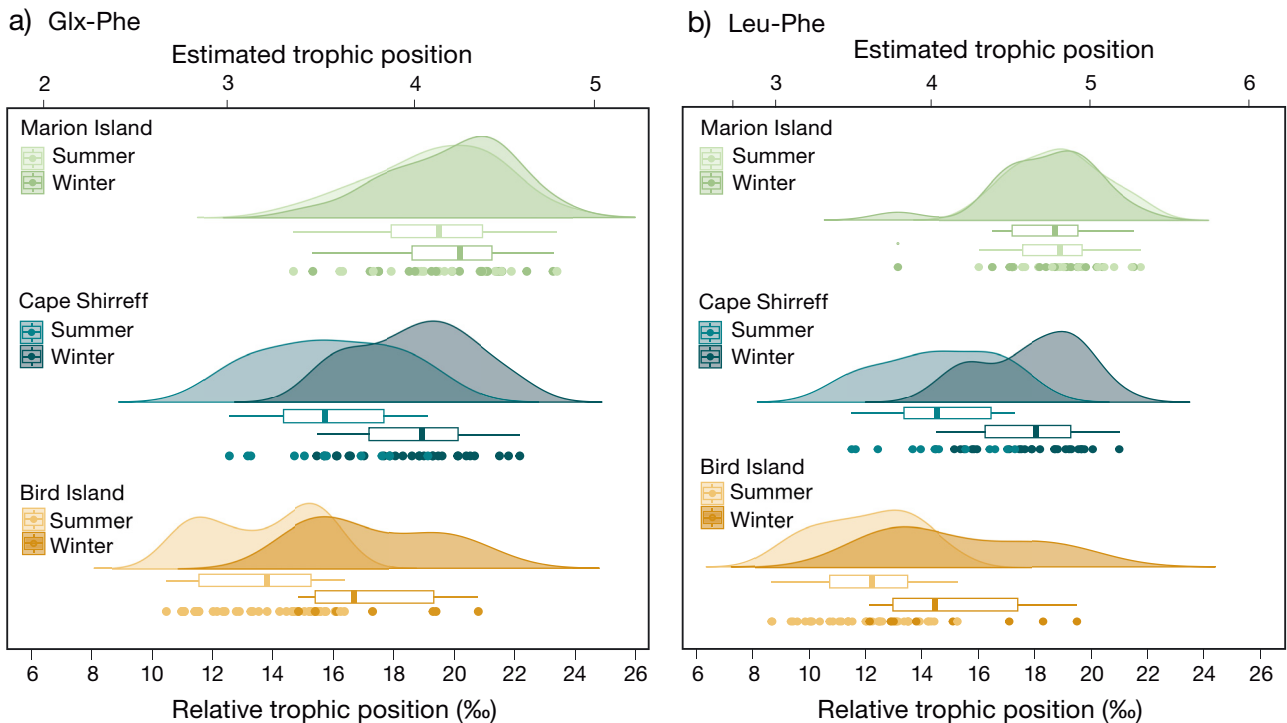


Fig. 5. Density distributions, boxplots (median, first and third quartile) and individual data points indicating the trophic position and relative trophic position of female Antarctic fur seals *Arctocephalus gazella* from Bird Island (summer $n = 41$, winter $n = 8$), Cape Shirreff (summer $n = 12$, winter $n = 26$) and Marion Island (summer $n = 21$, winter $n = 19$) during the summer and winter period. Estimated trophic position and relative trophic position were calculated using the glutamic acid or leucine (trophic) and phenylalanine (source) $\delta^{15}\text{N}$ values of whole blood samples

$\text{TP}_{\text{Glx-Phe}}$ ($y = 0.963 + 0.279x$, $r^2 = 0.473$, $p < 0.0001$) and $\text{TP}_{\text{Leu-Phe}}$ ($y = 0.794 + 0.354x$, $r^2 = 0.571$, $p < 0.0001$; Fig. 4). RTP varied from 10.5 to 23.4‰ for $\text{RTP}_{\text{Glx-Phe}}$ and from 8.7 to 21.8‰ for $\text{RTP}_{\text{Leu-Phe}}$ and followed the same trends as $\text{TP}_{\text{Glx-Phe}}$ and $\text{TP}_{\text{Leu-Phe}}$, respectively.

4. DISCUSSION

We used CSIA-AA to determine large-scale and seasonal variation in the food web baseline and trophic ecology of a wide-ranging Southern Ocean marine predator, the female AFS. We measured $\delta^{15}\text{N}_{\text{AA}}$ from 11 AAs, aligning with findings from prior CSIA-AA studies on Southern Ocean pinnipeds, including Weddell seals *Leptonychotes weddellii*, crabeater seals *Lobodon carcinophaga*, Ross seals *Ommatophoca rossii* (Brault et al. 2019) and southern elephant seals *Mirounga leonina* (Lübcker et al. 2020). Our results indicated that variations in bulk $\delta^{15}\text{N}$ values can be primarily attributed to changes in female AFS trophic ecology, with a smaller influence from changes in the isotopic baseline ($\delta^{15}\text{N}_{\text{baseline}}$). We demonstrated that $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ values of females from Marion Island are representative of the isotopic baseline in the Indian sector during both seasons, as compared to $\delta^{15}\text{N}_{\text{POM}}$ and $\delta^{15}\text{N}_{\text{PON}}$ values. Similarly, values of AFS females from Cape Shirreff are representative of the isotopic baseline of the northern Antarctic Peninsula in summer and of the southwest Atlantic sector in winter, as compared to $\delta^{15}\text{N}_{\text{POM}}$ values. In contrast, $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ of females from Bird Island were more ^{15}N -depleted than $\delta^{15}\text{N}_{\text{POM}}$ in summer. This suggests that our values may not accurately represent the isotopic baseline in this area in summer, whereas $\delta^{15}\text{N}_{\text{Phe}}$ values were comparable to $\delta^{15}\text{N}_{\text{POM}}$ in winter. These differences are likely due to complex biogeophysical processes around South Georgia, which are reflected in POM and seal blood due to their different isotopic turnover rate. Our compound-specific isotope approach to trophic dynamics revealed significant spatial and temporal differences in the trophic ecology of the AFS, consistent with previous diet studies. Notably, we observed a seasonal shift in the trophic ecology of females from Bird Island and Cape Shirreff, targeting higher trophic level prey in winter. Our results also highlight the utility of additional amino acids, such as Lys, alongside Phe for investigating isotopic baselines, and Leu for more accurate ecological TP estimations.

4.1. Basin-scale and seasonal variation in $\delta^{15}\text{N}$ baseline

Prior investigations into $\delta^{15}\text{N}_{\text{POM}}$ values in the Southern Ocean have identified complex seasonal and spatial variations compared to variation in $\delta^{13}\text{C}_{\text{POM}}$ (Espinasse et al. 2019, St John Glew et al. 2021). Our study, done on a seasonal and multi-basin scale, supports these findings. Collectively, our results indicate seasonal and spatial variations in the isotopic $\delta^{15}\text{N}$ baseline across the 3 ocean basins. In summer, we detected significant differences in $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ values between the Atlantic and Indian basins, with higher values for females from Marion Island, reflecting the local foraging behaviour of female AFSs in different water masses. Previous studies have identified differences in $\delta^{15}\text{N}_{\text{POM}}$ between Southern Ocean water masses, linked to variation in sea surface temperature, nitrogenous nutrients supporting net primary productivity, mixed layer depth and sea ice concentration, and delineated 2 major distinct biogeochemical regimes, i.e. north and south of the PF (Espinasse et al. 2019, St John Glew et al. 2021). During the summer season, females from Marion Island forage primarily within the SAZ (Wege et al. 2019), while females from higher-latitude Bird Island and Cape Shirreff forage south of the PF (Table 1). These differences in foraging zone use could explain the significantly higher $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ values for females from Marion Island. Moreover, as the Antarctic Circumpolar Current flows eastward, it transports essential nutrients like iron to phytoplankton communities, enhancing primary productivity in regions downstream of landmasses (Sergi et al. 2020). Phytoplankton preferentially take up ^{14}N nitrate, causing the residual pool to become progressively enriched in ^{15}N in productive areas (Lara et al. 2010, Sigman & Fripiat 2019). Consequently, observed differences in summer may also be explained by female AFS from Marion Island foraging preferentially south to southeast of the island (mostly downstream; Wege et al. 2019), while females from Bird Island and Cape Shirreff forage north–northwest of their island (upstream; Boyd et al. 2002, Staniland et al. 2010, Waluda et al. 2010, Borrás-Chávez 2020). We detected spatial differences in $\delta^{15}\text{N}_{\text{Lys}}$ values in winter, with $\delta^{15}\text{N}_{\text{Lys}}$ values from Bird Island significantly higher compared to the 2 other colonies, likely resulting from the wide-ranging movements of females (Fig. S3). Espinasse et al. (2019) also observed latitudinal variations in $\delta^{15}\text{N}_{\text{POM}}$ values in winter, but they noted a general decrease in values with increasing latitude in the Atlantic section. Our observed difference in this study may reflect variations in foraging locations rather than

a clear latitudinal gradient. Indeed, variation can be attributed to the females that fed over the Patagonian shelf break (Fig. S3). This region is recognized for its higher $\delta^{15}\text{N}_{\text{baseline}}$ values (Lara et al. 2010, Espinasse et al. 2019, Stirnimann et al. 2024), contributing to the overall increase in $\delta^{15}\text{N}_{\text{Lys}}$ values in winter.

Regarding seasonal variation within basins, the higher values of $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ in winter for females from Cape Shirreff can be attributed to females travelling west to the Pacific basin, and/or along the Chilean coast to the north of the SAF and the sub-Tropical Front (Fig. S3; Arthur et al. 2017, Hinke et al. 2017, Walters et al. 2020). Additionally, this variation may be explained by changes in the productivity of primary producers, as higher $\delta^{15}\text{N}_{\text{POM}}$ values have been predicted for the Chilean coast and near the Antarctic Peninsula between May and December (St John Glew et al. 2021). The absence of seasonal variation in $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ for seals from Marion Island aligns with seasonally stable $\delta^{15}\text{N}_{\text{POM}}$ values, found between 40° and 55° S (Espinasse et al. 2019), where most female AFSs foraged (Fig. S3).

The potential for using $\delta^{15}\text{N}$ values from source AAs of marine predators to monitor long-term changes in marine food web baselines has been highlighted by de la Vega et al. (2022). The $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ values for female AFS from Marion Island and Cape Shirreff are consistent with $\delta^{15}\text{N}_{\text{POM}}$ and $\delta^{15}\text{N}_{\text{PON}}$ values in their respective foraging areas (Seyboth et al. 2018, Espinasse et al. 2019, Smith et al. 2022, Stirnimann et al. 2024). The summer $\delta^{15}\text{N}_{\text{Phe}}$ values of females from Marion Island also align with those found in the lower beaks of Dana octopus squid *Taningia danae* ($0.8 \pm 1.6\text{‰}$; Cherel et al. 2019) and whole blood samples of southern rockhopper penguins *Eudyptes chrysocome chrysocome* (-0.2 to 1.8‰ ; Lorrain et al. 2009) sampled in the southern Indian Ocean. Taken together, our results suggest that $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ values can be used as reliable source AAs in the foraging regions of the Marion Island and Cape Shirreff AFS colonies and highlight their potential to monitor spatial and seasonal changes in the isotopic baseline of the Southern Ocean. It is important to note that the comparison for Cape Shirreff winter values was conducted using only $\delta^{15}\text{N}_{\text{POM}}$ data from the Atlantic sector. For a more precise comparison, it would be beneficial to include winter data from the Pacific sector, as some females also forage in this area (Fig. S3). However, to our knowledge, $\delta^{15}\text{N}_{\text{POM}}$ values for the Pacific sector in winter are unavailable at present.

During the winter, only $\delta^{15}\text{N}_{\text{Phe}}$ values were consistent with $\delta^{15}\text{N}_{\text{POM}}$ for females from Bird Island in the southern Atlantic basin. Differences between $\delta^{15}\text{N}_{\text{Phe}}$

and $\delta^{15}\text{N}_{\text{Lys}}$ values may be due to differences in AA turnover (McMahon & McCarthy 2016). In summer, $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ values of females from Bird Island were more ^{15}N -depleted than $\delta^{15}\text{N}_{\text{POM}}$, suggesting that our values may not accurately represent the isotopic baseline in this area. Although higher terrestrial inputs from Bird Island are unlikely to be significant in this context, nitrogen uptake processes on ^{15}N -depleted sources could be a contributing factor (Espinasse et al. 2019). Additionally, the observed differences might result from the different years in which samples were collected. Changes in water masses can influence $\delta^{15}\text{N}_{\text{baseline}}$ values (de la Vega et al. 2022), and the pelagic system around South Georgia is complex, characterized by considerable inter-annual variability (Hill et al. 2009). The complex patterns observed during summer may be attributed to disparate isotopic turnover, with POM exhibiting a fast isotopic turnover (Espinasse et al. 2019), while whole blood of marine predators has a longer turnover rate (several months; Cherel & Hobson 2007). Post-weaning of their pups, females are free from the constraints of lactation (Boyd et al. 2002) and forage across multiple frontal zones (Staniland et al. 2012, Arthur et al. 2017, Hinke et al. 2017, Wege et al. 2019) so that blood integrates isotopic compositions across multiple food web baselines. Consequently, $\delta^{15}\text{N}_{\text{POM}}$ and $\delta^{15}\text{N}_{\text{AA}}$ values from blood integrate baseline temporal variation over different time scales. To detect changes in the isotopic baseline in a specific area, it is important to consider the foraging range of the predator when using $\delta^{15}\text{N}_{\text{AA}}$ blood values. An alternative method would be to use $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ values from sequentially sampled keratinous tissues like whiskers that enable the reconstruction of an isotopic time-series that can be directly related to foraging areas at sea (Walters et al. 2020). Another explanation for the differences between $\delta^{15}\text{N}_{\text{Phe}}$, $\delta^{15}\text{N}_{\text{Lys}}$ and $\delta^{15}\text{N}_{\text{POM}}$ values could be that $\delta^{15}\text{N}_{\text{POM}}$ values may not accurately represent the $\delta^{15}\text{N}$ values of primary producers. Stable isotope data from POM have been used to provide isotopic baselines, but its suitability has been debated (St John Glew et al. 2021). Particulate organic matter comprises particles from various sources, not only phytoplankton, including faecal pellets of grazers (Soares et al. 2015), and therefore may not accurately represent what primary consumers are feeding on. Moreover, the composition of POM can vary significantly over time due to various processes such as microbial and grazing activity or water column stratification, raising questions about the reliability of POM as a food web baseline over large areas and medium- to long-term changes in

marine ecosystems (St John Glew et al. 2021, Espinasse et al. 2022). Finally, despite recent publications on $\delta^{15}\text{N}_{\text{POM}}$ in the Southern Ocean (Espinasse et al. 2019, Stirnimann et al. 2024), there is still a lack of reference data available for some regions (e.g. Pacific) and seasons (especially winter), which limited our comparisons and conclusions in this study.

4.2. Basin-scale and seasonal variation in the trophic ecology of AFS

We observed spatial differences in $\delta^{15}\text{N}_{\text{Glx}}$, $\delta^{15}\text{N}_{\text{Leu}}$, $\text{TP}_{\text{Glx-Phe}}$, $\text{TP}_{\text{Leu-Phe}}$, $\text{RTP}_{\text{Glx-Phe}}$ and $\text{RTP}_{\text{Leu-Phe}}$ during both seasons. Our results suggest that, in summer, females from Marion Island feed on higher trophic level prey compared to females from Bird Island and Cape Shirreff. Marion Island AFSs had TP values indicative of predation on myctophids (average TP value of 2.9; Choy et al. 2012) and squids, likely including *Filippovia knipovitchi* (average TP value of 4.1; Woods et al. 2022). In contrast, TP values of females from Bird Island indicate a diet predominantly consisting of Antarctic krill (average TP value of 2.3; Conroy et al. 2024). These findings are consistent with previous scat analysis studies (Table 1; Reid & Arnould 1996, Klages & Bester 1998, Brown et al. 1999, Makhado et al. 2008, Polito & Goebel 2010, Reisinger et al. 2018, Borrás-Chávez 2020). Fur seals from Cape Shirreff had TP values in summer consistent with predation on krill as expected, but also on myctophids and squids, likely including *Martialia hyades* (TP values ranging from 2.7 to 3.7; Woods et al. 2022). AFSs from Cape Shirreff primarily rely on Antarctic krill as their main food source in summer, but there are indications of a dietary shift towards myctophids and squid prior to parturition and when krill availability is limited (Polito & Goebel 2010, Krause et al. 2022). Interestingly, in winter, Cape Shirreff females showed higher TP compared to Bird Island females but were comparable to that of Marion Island females. The higher TPs may result from females incorporating more myctophids and squids into their diet, due to a decrease in krill availability. Additionally, a shift in the diet of krill, which feed at higher trophic levels in autumn/winter (Zhu et al. 2018), could also result in higher TP values. Another factor that needs consideration is the vertical foraging of AFS, as this can influence $\delta^{15}\text{N}$ values in their tissues. However, previous studies have shown that females are relatively shallow divers, with an average dive depth within the first 20 m and maximum diving depth of 200 m (Arthur et al. 2016).

Regarding seasonal variations, our results indicate no significant differences in $\delta^{15}\text{N}_{\text{Leu}}$, $\text{TP}_{\text{Leu-Phe}}$ and $\text{RTP}_{\text{Leu-Phe}}$ between summer and winter for females from Marion Island. During mid-winter, some female AFSs from Marion Island have been reported foraging south of the PF near the ice edge (Fig. S3; Arthur et al. 2017, Wege et al. 2019). Corresponding bulk stable isotope values in whiskers revealed that they are targeting lower trophic level prey, likely Antarctic krill (Walters 2014, Walters et al. 2020). In our study, one female in winter showed a TP below 4, which is consistent with feeding on krill (average TP value of 2.3 for Antarctic krill; Conroy et al. 2024). The absence of seasonal differences could be due to only a small portion of females feeding on krill, or as whole blood reflects seal diet only at the end of the inter-breeding foraging trip, it limits the ability to detect long-term dietary trends, such as mid-winter krill consumption. The TPs of females from Marion Island are in the same range as those calculated for Dana octopus squid (4.8 ± 0.3) and colossal squid *Mesonychoteuthis hamiltoni* (4.7 ± 0.3) beaks sampled in the southern Indian Ocean (Cherel et al. 2019), indicating that female AFSs likely occupy a similar position in the food web.

Significant seasonal differences in $\delta^{15}\text{N}_{\text{Leu}}$, $\text{TP}_{\text{Leu-Phe}}$ and $\text{RTP}_{\text{Leu-Phe}}$ were detected for females from Bird Island in the south Atlantic sector, indicating that females occupied a higher $\text{TP}_{\text{Leu-Phe}}$ in winter. This is consistent with tracking studies (Boyd et al. 2002) and scat analysis (Reid 1995, Reid & Arnould 1996). A study analysing scats of female AFSs from Bird Island during the same years as this study (2008–2010) revealed a higher frequency of krill in their diet during summer (79%) when most of our females had a $\text{TP}_{\text{Leu-Phe}}$ between 3 and 4 (Coleman 2022). In contrast, during winter, fish made an increased contribution to their diet (57%), with half of the females having a $\text{TP}_{\text{Leu-Phe}}$ below 4 and the other half a $\text{TP}_{\text{Leu-Phe}}$ above 4 (Coleman 2022). A seasonal shift in $\text{TP}_{\text{Leu-Phe}}$ is consistent with a change in diet composition as observed from scat analysis.

The distribution of $\text{TP}_{\text{Leu-Phe}}$ and RTP among females from Bird Island indicates the existence of several predominant feeding strategies within the population. In summer, one group exhibits RTP between 8 and 12‰, another between 12 and 16‰, and in winter, a third group between 16 and 20‰ (Fig. 4). Previous studies using stable isotope analysis on whiskers revealed niche partitioning among females from the same colony (Jones et al. 2020, Walters et al. 2020). Jones et al. (2020) estimated during winter that approximately 30% foraged to the north of the PF, primarily consuming squid, myctophids and other

fishes, while the remaining 70% foraged to the south of the PF, feeding on large quantities of Antarctic krill. In addition, in warmer years with reduced krill availability, females from Bird Island tend to consume more squid (McCafferty et al. 1998, Abreu et al. 2019). The large population of AFSs at South Georgia (Bird Island), accounting for 95% of the global population, may lead to intra-specific competition and resource partitioning among females to relax competition (Jones et al. 2020). Intra-population niche partitioning also appears to be present among females from Cape Shirreff (Fig. 4). Borrás-Chávez (2020) described 2 distinct dietary clusters among these females in summer: one was characterized by a krill-dominated diet and the other by a fish-dominated diet. Our results confirm these findings and further reveal that, in winter, the TP and RTP distributions also indicate 2 main groups. One group has $RTP_{Leu-Phe}$ between 15 and 16, indicative of primarily feeding on myctophids, while the other larger group has $RTP_{Leu-Phe}$ values between 17 and 21, which suggest a diet more focused on squid.

4.3. Advances and challenges in using AAs for studying wide-ranging marine predators

Accurate dietary assessment of marine predators is needed to detect spatial and temporal variations in predator–prey relationships in the Southern Ocean. Our study highlights the importance of using CSIA-AA for detecting spatial trophic variations in trophic ecology of marine predators. While spatial differences in the AFS trophic ecology between Bird Island and Cape Shirreff in summer, and between Marion Island and Bird Island in winter, were detected with $\delta^{15}N_{AA}$ values, they were not observed with $\delta^{15}N_{bulk}$ values. The metabolic AA Thr, along with Leu, were the only AAs to differentiate between the 3 colonies in summer, and Bird Island from the 2 other colonies in winter, suggesting that Thr is a useful ecological biomarker to support robust comparisons of spatial and temporal variability in consumer trophic ecology (Lübcker et al. 2020).

While Glu and Phe have traditionally been the primary AAs used in studies, we show the potential value of incorporating additional AAs into isotopic baseline and trophic ecology investigations of marine predators (McMahon et al. 2015b). Lys could also serve as an informative source AA (Nielsen et al. 2015), as $\delta^{15}N_{Lys}$ values revealed differences in baselines between Marion Island and Cape Shirreff in summer, as well as between Bird Island and the 2 other colonies in

winter, which were non-detected by $\delta^{15}N_{Phe}$ values. Additionally, we showed that $\delta^{15}N_{Lys}$ is more representative of the isotopic baseline compared to $\delta^{15}N_{Phe}$ during this season for Marion Island AFSs. The differences in $\delta^{15}N_{Phe}$ and $\delta^{15}N_{Lys}$ values can be attributed to their distinct metabolic pathways. Lys metabolism is unique due to the presence of 2 nitrogen groups. While there are several pathways for Lys catabolism, the primary pathway in mammals involves irreversible transamination. In contrast, Phe has 2 potential catabolic routes: a minor pathway involving transamination, and a dominant pathway involving hydroxylation to tyrosine (McMahon & McCarthy 2016, O'Connell 2017).

Additionally, we found that $TP_{Leu-Phe}$ (as opposed to the widely used $TP_{Glx-Phe}$) provided the most ecologically realistic TP estimation for female AFSs, given that, as secondary and tertiary consumers (depending on their diet), it is ecologically impossible for AFSs to have a TP below 3.0. Moreover, average $TP_{Leu-Phe}$ estimates for Marion Island (4.7 in summer and 4.8 in winter) are close to TP_{bulk} estimated for females from the Kerguelen Islands (4.8 ± 0.1 ; Cherel et al. 2010), which have a similar diet and forage within the same ocean basin. In contrast, 33% of females from Bird Island exhibited $TP_{Glu-Phe}$ below 3.0, a TP unrealistically low for AFSs. Previous studies on crabeater seals and squids have also documented TPs below 3.0 (Brault et al. 2019, Woods et al. 2020, 2022). These findings underscore the persistent challenges in relying on absolute TP values and in the parameterization of TP equations. Additionally, we observed low TPs (<4.0) for some female AFSs from Marion Island in summer, which are thought to primarily feed on myctophid fish during this season (Makhado et al. 2008). These low TP estimates may also be due to the TP estimation method used, or alternatively, it may suggest that those females predated on organisms at lower trophic levels than previously assumed during the summer. However, as scat analysis is known to be biased to prey with hard parts, alternative genetic (DNA) metabarcoding analysis of scat samples from females from Marion Island could provide valuable insights into prey consumption (Augé et al. 2012, McInnes et al. 2017, Cavallo et al. 2018).

Another challenge is the absence of an AFS-specific TDF; however, Borrell et al. (2012) suggested that TDFs remain relatively consistent among taxonomically closely related species, making the harbour seal the most suitable option for our study. This underscores the need for TDF and β estimates specific to AFS or at least for more closely related species. While the inclusion of RTP values can provide a more stand-

ardized approached, it does not eliminate the issue of unknown TDF variability.

5. PERSPECTIVES AND CONCLUSIONS

Long-term studies encompassing spatiotemporal variability in the structure and function of the Southern Ocean ecosystem across all of its sectors are essential (Constable et al. 2023). Considering the recent major changes in AFS populations (Krause et al. 2022, 2024, Forcada et al. 2023), and the pronounced inter-annual and intra-colony variability (Trathan et al. 2021), exploring long-term variability in the food web baseline and trophic ecology of AFSs across Southern Ocean sectors can provide insight into the environmental changes happening in Southern Ocean food webs (Huang et al. 2011, de Lima et al. 2022). Recent long-term studies have highlighted changes in phytoplankton phenology and bloom duration in the Southern Ocean (Thomalla et al. 2023, Antoni et al. 2024). For example, Antoni et al. (2024) revealed significant changes in phytoplankton communities in the western Antarctic Peninsula region between 2010 and 2020, including the detection of a nanoplankton species from temperate waters (Antoni et al. 2024). Changes in the food web baseline can impact the overall food web structure, and such changes have been detected in marine predator isotopic signatures (de la Vega et al. 2022, 2023). Our study provides valuable baseline data for the detection of future changes in local food webs.

Our findings provide further evidence of the complex spatial and seasonal variations in the $\delta^{15}\text{N}$ baseline in the Southern Ocean and highlight both the advantages and limitations of using $\delta^{15}\text{N}$ from source AAs of a marine predator to detect them. While $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ values from Marion Island and Cape Shirreff females were consistent with $\delta^{15}\text{N}_{\text{POM}}$ and $\delta^{15}\text{N}_{\text{PON}}$ values in the Indian and Atlantic sector during both seasons, the area of the Atlantic sector around Bird Island exhibited a more complex pattern. The wide range of foraging behaviours of AFSs in winter, complex spatial and seasonal variations in processes influencing $\delta^{15}\text{N}$ at the base of the food web, possible discrepancies between $\delta^{15}\text{N}$ of source AAs, $\delta^{15}\text{N}_{\text{POM}}$ and $\delta^{15}\text{N}_{\text{baseline}}$, and the lack of data in winter and in the Pacific basin suggest the need for cautious interpretation and further research to improve the reliability of $\delta^{15}\text{N}_{\text{baseline}}$ estimates. Nonetheless, our method provides greater insight into variations in the isotopic baseline in the Southern Ocean and the foraging ecology of the AFS, including the poorly sam-

pled winter season, emphasizing the importance of a comprehensive understanding of seasonal dynamics in the region, and providing a baseline for future CSIA-AA studies. AFSs occupy a diverse range of TPs, encompassing more than 2 trophic levels. This highlights the intra- and inter-colony flexibility in the diet and trophic role of female AFSs, and the importance of considering individual and regional variability in populations for management, conservation, and ecosystem models of the Southern Ocean.

Acknowledgements. Funding from the Australian Research Council (ARC) Discovery Scheme supported this research (DP0770910, DP210100604). N.F. was supported by the ARC's Special Research Initiative for the Antarctic Gateway Partnership (Project ID SR140300001). A.W. was supported by the ARC DP210100604. This project was made possible by the collaboration and support of the University of Pretoria and the South African National Antarctic Program (SANAP), the British Antarctic Survey (BAS), and the US Antarctic Marine Living Resources (US AMLR) Program. We are grateful for the field and technical support provided by E. Edwards, D. Malone, I. Staniland, M. Postma, R. Burner, C. Bonin, S. Freeman, R. Buchheit, N. Pussini, A. Takahashi and field assistants of the Marion Island Marine Mammal Programme. Laboratory support for amino acid extractions and analysis was provided by Mina Brock. We gratefully acknowledge B. Arthur for data support, Shane Richards for his invaluable assistance with the statistical analysis and Kelton McMahon as well as an anonymous reviewer for their expertise. This collaboration was initiated while one of the co-authors (Michael E. Goebel) was directing pinniped studies for the US Antarctic Marine Living Resources, Southwest Fisheries Science Center, NOAA. The work presented in this paper occurred during his current affiliation (cited above).

LITERATURE CITED

- ✦ Abraham JP, Baringer M, Bindoff NL, Boyer T and others (2013) A review of global ocean temperature observations: implications for ocean heat content estimates and climate change. *Rev Geophys* 51:450–483
- ✦ Abreu J, Staniland I, Rodrigues CF, Queirós JP, Pereira JM, Xavier JC (2019) Squid in the diet of Antarctic fur seals: potential links to oceanographic conditions and Antarctic krill abundance. *Mar Ecol Prog Ser* 628:211–221
- ✦ Antoni JS, Almandoz GO, Goldsmit J, Garcia MD, Flores-Melo X, Hernando MP, Schloss IR (2024) Long-term studies on West Antarctic Peninsula phytoplankton blooms suggest range shifts between temperate and polar species. *Glob Change Biol* 30:e17238
- ✦ Arthur B, Hindell M, Bester MN, Oosthuizen WC, Wege M, Lea MA, Costa D (2016) South for the winter? Within-divide foraging effort reveals the trade-offs between divergent foraging strategies in a free-ranging predator. *Funct Ecol* 30:1623–1637
- ✦ Arthur B, Hindell M, Bester M, De Bruyn PJN, Trathan P, Goebel M, Lea MA (2017) Winter habitat predictions of a key Southern Ocean predator, the Antarctic fur seal (*Arctocephalus gazella*). *Deep Sea Res II* 140:171–181

- Asch RG (2019) Changing seasonality of the sea: past, present, and future. In: Cisneros-Montemayor AM, Cheung WWL, Ota Y (eds) Predicting future oceans. Elsevier, Amsterdam, p 39–51
- ✦ Augé AA, Lalas C, Davis LS, Chilvers BL (2012) Autumn diet of recolonising female New Zealand sea lions based at Otago Peninsula, South Island, New Zealand. *NZ J Mar Freshw Res* 46:97–110
- ✦ Bates D, Machler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67: 1–48
- ✦ Bailleul F, Luque S, Dubroca L, Arnould JPY, Guinet C (2005) Differences in foraging strategy and maternal behaviour between two sympatric fur seal species at the Crozet Islands. *Mar Ecol Prog Ser* 293:273–282
- ✦ Bestley S, Ropert-Coudert Y, Bengtson Nash S, Brooks CM and others (2020) Marine ecosystem assessment for the Southern Ocean: birds and marine mammals in a changing climate. *Front Ecol Evol* 8:566936
- ✦ Boecklen WJ, Yarnes CT, Cook BA, James AC (2011) On the use of stable isotopes in trophic ecology. *Annu Rev Ecol Syst* 42:411–440
- ✦ Bonnet-Lebrun AS, Sweetlove M, Griffiths HJ, Sumner M and others (2023) Opportunities and limitations of large open biodiversity occurrence databases in the context of a Marine Ecosystem Assessment of the Southern Ocean. *Front Mar Sci* 10:1150603
- Borrás-Chávez RF (2020) Living in the fast lane: foraging ecology of the Antarctic fur seal (*Arctocephalus gazella*) at the edge of their breeding distribution. PhD dissertation, Pontificia Universidad Católica de Chile, Santiago
- ✦ Borrell A, Abad-Oliva N, Gomez-Campos E, Gimenez J, Aguilar A (2012) Discrimination of stable isotopes in fin whale tissues and application to diet assessment in cetaceans. *Rapid Commun Mass Spectrom* 26:1596–1602
- ✦ Boyd IL, Staniland IJ, Martin AR (2002) Distribution of foraging by female Antarctic fur seals. *Mar Ecol Prog Ser* 242: 285–294
- ✦ Brault EK, Koch PL, Costa DP, McCarthy MD and others (2019) Trophic position and foraging ecology of Ross, Weddell, and crabeater seals revealed by compound-specific isotope analysis. *Mar Ecol Prog Ser* 611:1–18
- ✦ Breitburg D, Levin LA, Oshlies A, Gregoire M and others (2018) Declining oxygen in the global ocean and coastal waters. *Science* 359:eaam7240
- ✦ Brown DJ, Boyd IL, Cripps GC, Butler PJ (1999) Fatty acid signature analysis from the milk of Antarctic fur seals and Southern elephant seals from South Georgia: implications for diet determination. *Mar Ecol Prog Ser* 187:251–263
- ✦ Carpenter-Kling T, Handley JM, Connan M, Crawford RJM and others (2019) Gentoo penguins as sentinels of climate change at the sub-Antarctic Prince Edward Archipelago, Southern Ocean. *Ecol Indic* 101:163–172
- ✦ Carpenter-Kling T, Pistorius P, Reisinger R, Cherel Y, Connan M (2020) A critical assessment of marine predator isoscapes within the southern Indian Ocean. *Mov Ecol* 8:29
- ✦ Casaux R, Baroni A, Arrighetti F, Ramón A, Carlini A (2003) Geographical variation in the diet of the Antarctic fur seal *Arctocephalus gazella*. *Polar Biol* 26:753–758
- ✦ Casaux R, Juarez M, Carlini A, Corbalán A (2016) The diet of the Antarctic fur seal *Arctocephalus gazella* at the South Orkney Islands in ten consecutive years. *Polar Biol* 39: 1197–1206
- ✦ Cavallo C, Chiaradia A, Deagle BE, McInnes JC, Sánchez S, Hays GC, Reina RD (2018) Molecular analysis of predator scats reveals role of salps in temperate inshore food webs. *Front Mar Sci* 5:381
- ✦ Cavanagh RD, Melbourne-Thomas J, Grant SM, Barnes DKA and others (2021) Future risk for Southern Ocean ecosystem services under climate change. *Front Mar Sci* 7:615214
- ✦ Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar Ecol Prog Ser* 329:281–287
- ✦ Cherel Y, Fontaine C, Richard P, Labatc JP (2010) Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. *Limnol Oceanogr* 55: 324–332
- ✦ Cherel Y, Bustamante P, Richard P (2019) Amino acid $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from sclerotized beaks: a new tool to investigate the foraging ecology of cephalopods, including giant and colossal squids. *Mar Ecol Prog Ser* 624:89–102
- ✦ Chikaraishi Y, Kashiyama Y, Ogawa NO, Kitazato H, Ohkouchi N (2007) Metabolic control of nitrogen isotope composition of amino acids in macroalgae and gastropods: implications for aquatic food web studies. *Mar Ecol Prog Ser* 342:85–90
- ✦ Chikaraishi Y, Ogawa NO, Kashiyama Y, Takano Y and others (2009) Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. *Limnol Oceanogr Methods* 7:740–750
- ✦ Choy CA, Davison PC, Drazen JC, Flynn A and others (2012) Global trophic position comparison of two dominant mesopelagic fish families (Myctophidae, Stomiidae) using amino acid nitrogen isotopic analyses. *PLOS ONE* 7:e50133
- ✦ Choy CA, Popp BN, Hannides CCS, Drazen JC (2015) Trophic structure and food resources of epipelagic and mesopelagic fishes in the North Pacific Subtropical Gyre ecosystem inferred from nitrogen isotopic compositions. *Limnol Oceanogr* 60:1156–1171
- Coleman J (2022) Spatiotemporal variability in Antarctic krill (*Euphausia superba*) around South Georgia from Antarctic fur seal (*Arctocephalus gazella*) diets at two long term monitoring sites. MSc dissertation, University College Cork
- ✦ Conroy JA, Steinberg DK, Nardelli SC, Schofield O (2024) Omnivorous summer feeding by juvenile Antarctic krill in coastal waters. *Limnol Oceanogr* 69:874–887
- ✦ Constable AJ (2003) Southern Ocean productivity in relation to spatial and temporal variation in the physical environment. *J Geophys Res* 108:1–21
- ✦ Constable AJ, Melbourne-Thomas J, Corney SP, Arrigo KR and others (2014) Climate change and Southern Ocean ecosystems. I. How changes in physical habitats directly affect marine biota. *Glob Change Biol* 20:3004–3025
- Constable AJ, Melbourne-Thomas J, Muelbert MMC, McCormack S and others (2023) Marine ecosystem assessment for the Southern Ocean: summary for policymakers. Integrated climate and ecosystem dynamics in the Southern Ocean. Scientific Committee on Antarctic Research, Scientific Committee on Oceanic Research, Integrated Marine Biosphere Research, doi:10.5281/zenodo.8359585
- ✦ Crowder L, Norse E (2008) Essential ecological insights for marine ecosystem-based management and marine spatial planning. *Mar Policy* 32:772–778
- De Broyer C, Koubbi P, Griffiths HJ, Raymond B and others (2014) Conclusions: present and future of Southern

- ocean biogeography. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B and others (eds) Biogeographic atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, p 470–475
- de la Vega C, Buchanan PJ, Tagliabue A, Hopkins JE and others (2022) Multi-decadal environmental change in the Barents Sea recorded by seal teeth. *Glob Change Biol* 28: 3054–3065
- de la Vega C, Kershaw J, Stenson GB, Frie AK and others (2023) Multi-decadal trends in biomarkers in harp seal teeth from the North Atlantic reveal the influence of prey availability on seal trophic position. *Glob Change Biol* 29: 5582–5595
- de Lima RC, Cebuhar JD, Negrete J, Ferreira A, Secchi ER, Botta S (2022) Ecosystem shifts inferred from long-term stable isotope analysis of male Antarctic fur seal *Arctocephalus gazella* teeth. *Mar Ecol Prog Ser* 695:203–216
- DeNiro MJ, Epstein SE (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351
- DiFiore PJ, Sigman DM, Karsh KL, Trull TW, Dunbar RB, Robinson RS (2010) Poleward decrease in the isotope effect of nitrate assimilation across the Southern Ocean. *Geophys Res Lett* 37:L17601
- Espinasse B, Pakhomov EA, Hunt BPV, Bury SJ (2019) Latitudinal gradient consistency in carbon and nitrogen stable isotopes of particulate organic matter in the Southern Ocean. *Mar Ecol Prog Ser* 631:19–30
- Espinasse B, Sturbois A, Basedow SL, Hélaouët P, Johns DG, Newton J, Trueman CN (2022) Temporal dynamics in zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes for the North Atlantic Ocean: decadal cycles, seasonality, and implications for predator ecology. *Front Ecol Evol* 10:986082
- Feddern ML, Ward EJ, Warlick AJ, Holtgrieve GW (2022) Recent divergent changes in Alaskan pinniped trophic position detected using compound-specific stable isotope analysis. *Mar Ecol Prog Ser* 688:153–166
- Forcada J, Staniland IJ (2009) Antarctic fur seal: *Arctocephalus gazella*. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of marine mammals, Vol 2. Academic Press, San Diego, CA, p 36–42
- Forcada J, Hoffman JI, Gimenez O, Staniland IJ, Bucktrout P, Wood AG (2023) Ninety years of change, from commercial extinction to recovery, range expansion and decline for Antarctic fur seals at South Georgia. *Glob Change Biol* 29:6867–6887
- Germain LR, Koch PL, Harvey J, McCarthy MD (2013) Nitrogen isotope fractionation in amino acids from harbor seals: implications for compound-specific trophic position calculations. *Mar Ecol Prog Ser* 482:265–277
- Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioules D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping. Springer, Dordrecht, p 299–318
- Guinet C, Dubroca L, Lea MA, Goldsworthy S and others (2001) Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Mar Ecol Prog Ser* 219: 251–264
- Harrington A, Daneri GA, Carlini AR, Reygert DS, Corbalán A (2017) Seasonal variation in the diet of Antarctic fur seals, *Arctocephalus gazella*, at 25 de Mayo/King George Island, South Shetland Islands, Antarctica. *Polar Biol* 40: 471–475
- Hazen EL, Abrahms B, Brodie S, Carroll G and others (2019) Marine top predators as climate and ecosystem sentinels. *Front Ecol Environ* 17:565–574
- Hilderbrand GV, Farley SD, Robbins CT, Hanley TA, Titus K, Servheen C (1996) Use of stable isotopes to determine diets of living and extinct bears. *Can J Zool* 74:2080–2088
- Hill S, Belchier M, Collins M, Fielding S and others (2009) Multiple indicators suggest a strong ecosystem anomaly at South Georgia in 2009. WG-EMM-09/23. CCAMLR. <https://meetings.ccamlr.org/en/wg-emm-09/23>
- Hinke JT, Cossio AM, Goebel ME, Reiss CS, Trivelpiece WZ, Watters GM (2017) Identifying risk: concurrent overlap of the Antarctic krill fishery with krill-dependent predators in the Scotia Sea. *PLOS ONE* 12:e0170132
- Huang T, Sun L, Stark J, Wang Y, Cheng Z, Yang Q, Sun S (2011) Relative changes in krill abundance inferred from Antarctic fur seal. *PLOS ONE* 6:e27331
- Jennings S, Warr KJ (2003) Environmental correlates of large-scale spatial variation in the $\delta^{15}\text{N}$ of marine animals. *Mar Biol* 142:1131–1140
- Jones KA, Ratcliffe N, Votier SC, Newton J and others (2020) Intra-specific niche partitioning in Antarctic fur seals, *Arctocephalus gazella*. *Sci Rep* 10:3238
- Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Can J Zool* 78:1–27
- Klages NTW, Bester MN (1998) Fish prey of fur seals *Arctocephalus* spp. at subantarctic Marion Island. *Mar Biol* 131:559–566
- Krause DJ, Bonin CA, Goebel ME, Reiss CS, Watters GM (2022) The rapid population collapse of a key marine predator in the Northern Antarctic Peninsula endangers genetic diversity and resilience to climate change. *Front Mar Sci* 8:796488
- Krause DJ, Brownell RL Jr, Bonin CA, Woodman SM, Shaftel D, Watters GM (2024) Evaluating threats to South Shetland Antarctic fur seals amidst population collapse. *Mamm Rev* 54:30–46
- Lara RJ, Alder V, Franzosi CA, Kattner G (2010) Characteristics of suspended particulate organic matter in the southwestern Atlantic: influence of temperature, nutrient and phytoplankton features on the stable isotope signature. *J Mar Syst* 79:199–209
- Lorrain A, Graham B, Ménard F, Popp B, Bouillon S, van Breugel P, Cherel Y (2009) Nitrogen and carbon isotope values of individual amino acids: a tool to study foraging ecology of penguins in the Southern Ocean. *Mar Ecol Prog Ser* 391:293–306
- Lorrain A, Graham BS, Popp BN, Allain V and others (2015) Nitrogen isotopic baselines and implications for estimating foraging habitat and trophic position of yellowfin tuna in the Indian and Pacific Oceans. *Deep Sea Res II* 113:188–198
- Lübcker N, Whiteman JP, Millar RP, de Bruyn PJN, Newsome SD (2020) Fasting affects amino acid nitrogen isotope values: a new tool for identifying nitrogen balance of free-ranging mammals. *Oecologia* 193:53–65
- Lübcker N, Newsome SD, Bester MN, de Bruyn PJN (2021) Validating the use of bulk tissue stable isotope and amino acid $\delta^{15}\text{N}$ values measured in molted hair and epidermis of elephant seals to assess temporal foraging niche specialization. *Mar Ecol Prog Ser* 673:229–243

- MacKenzie KM, Robertson DR, Adams JN, Altieri AH, Turner BL (2019) Structure and nutrient transfer in a tropical pelagic upwelling food web: from isoscapes to the whole ecosystem. *Prog Oceanogr* 178:102145
- Magozzi S, Thorrold SR, Houghton L, Bendall VA and others (2021) Compound-specific stable isotope analysis of amino acids in pelagic shark vertebrae reveals baseline, trophic, and physiological effects on bulk protein isotope records. *Front Mar Sci* 8:673016
- Makhado AB, Bester MN, Kirkman SP, Pistorius PA, Ferguson JWH, Klages NTW (2008) Prey of the Antarctic fur seal *Arctocephalus gazella* at Marion Island. *Polar Biol* 31: 575–581
- McCafferty DJ, Boyd IL, Walker TR, Taylor RI (1998) Foraging responses of Antarctic fur seals to changes in the marine environment. *Mar Ecol Prog Ser* 166: 285–299
- McClelland JW, Montoya JP (2002) Trophic relationships and the nitrogen isotopic composition of amino acids in plankton. *Ecology* 83:2173–2180
- McCormack SA, Melbourne-Thomas J, Trebilco R, Griffith G and others (2021) Southern Ocean food web modelling: progress, prognoses, and future priorities for research and policy makers. *Front Ecol Evol* 9:624763
- McInnes JC, Alderman R, Lea MA, Raymond B and others (2017) High occurrence of jellyfish predation by black-browed and Campbell albatross identified by DNA metabarcoding. *Mol Ecol* 26:4831–4845
- McMahon KW, McCarthy MD (2016) Embracing variability in amino acid $\delta^{15}\text{N}$ fractionation: mechanisms, implications, and applications for trophic ecology. *Ecosphere* 7: e01511
- McMahon KW, Newsome SD (2019) Amino acid isotope analysis: a new frontier in studies of animal migration and foraging ecology. In: Hobson KA, Wassenaar LI (eds) *Tracking animal migration with stable isotopes*, 2nd edn. Academic Press, London, p 173–190
- McMahon KW, Hamady LL, Thorrold SR (2013) A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnol Oceanogr* 58:697–714
- McMahon KW, Thorrold SR, Elsdon TS, McCarthy MD (2015) Trophic discrimination of nitrogen stable isotopes in amino acids varies with diet quality in a marine fish. *Limnol Oceanogr* 60:1076–1087
- McMahon KW, Michelson CI, Hart T, McCarthy MD, Patterson WP, Polito MJ (2019) Divergent trophic responses of sympatric penguin species to historic anthropogenic exploitation and recent climate change. *Proc Natl Acad Sci USA* 116:25721–25727
- Meekan MG, Virtue P, Marcus L, Clements KD, Nichols PD, Revill AT (2022) The world's largest omnivore is a fish. *Ecology* 103:e3818
- Moore CM, Mills MM, Arrigo KR, Berman-Frank I and others (2013) Processes and patterns of oceanic nutrient limitation. *Nat Geosci* 6:701–710
- Nielsen JM, Popp BN, Winder M (2015) Meta-analysis of amino acid stable nitrogen isotope ratios for estimating trophic position in marine organisms. *Oecologia* 178: 631–642
- O'Connell TC (2017) 'Trophic' and 'source' amino acids in trophic estimation: a likely metabolic explanation. *Oecologia* 184:317–326
- Osman LP, Hucke-Gaete R, Moreno CA, Torres D (2004) Feeding ecology of Antarctic fur seals at Cape Shirreff, South Shetlands, Antarctica. *Polar Biol* 27:92–98
- Park YH, Park T, Kim TW, Lee SH and others (2019) Observations of the Antarctic Circumpolar Current over the Udintsev Fracture Zone, the narrowest choke point in the Southern Ocean. *J Geophys Res Oceans* 124: 4511–4528
- Pecl GT, Araujo MB, Bell JD, Blanchard J and others (2017) Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355: eaai9214
- Pethybridge H, Choy CA, Logan JM, Allain V and others (2018a) A global meta-analysis of marine predator nitrogen stable isotopes: relationships between trophic structure and environmental conditions. *Glob Ecol Biogeogr* 27:1043–1055
- Pethybridge HR, Choy CA, Polovina JJ, Fulton EA (2018b) Improving marine ecosystem models with biochemical tracers. *Annu Rev Mar Sci* 10:199–228
- Polito MJ, Goebel ME (2010) Investigating the use of stable isotope analysis of milk to infer seasonal trends in the diets and foraging habitats of female Antarctic fur seals. *J Exp Mar Biol Ecol* 395:1–9
- Poloczanska ES, Burrows MT, Brown CJ, García Molinos J and others (2016) Responses of marine organisms to climate change across Oceans. *Front Mar Sci* 3:62
- Popp BN, Graham BS, Olson RJ, Hannides CCS and others (2007) Insight into the trophic ecology of yellowfin tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. In: Dawson TE, Siegwolf RTW (eds) *Stable isotopes as indicators of ecological change*. *Terrestrial Ecology Vol 1*. Academic Press, Amsterdam, p 173–190
- Post DM (2002) Using stable isotopes to estimate trophic position model, methods, and assumptions. *Ecology* 83: 703–718
- R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org/
- Ramirez MD, Besser AC, Newsome SD, McMahon KW (2021) Meta-analysis of primary producer amino acid $\delta^{15}\text{N}$ values and their influence on trophic position estimation. *Methods Ecol Evol* 12:1750–1767
- Reid K (1995) The diet of Antarctic fur seals (*Arctocephalus gazella* Peters 1875) during winter at South Georgia. *Antarct Sci* 7:241–249
- Reid K, Arnould JPY (1996) The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biol* 16:105–114
- Reisinger RR, Landman M, Mgibantaka N, Smale MJ, Bester MN, De Bruyn PJN, Pistorius PA (2018) Overlap and temporal variation in the diets of sympatric Antarctic and subantarctic fur seals (*Arctocephalus* spp.) at Marion Island, Prince Edward Islands. *Polar Res* 37:1451142
- Rita D, Borrell A, Wodarg D, Vikingsson G, García-Vernet R, Aguilar A, Loick-Wilde N (2024) Amino acid-specific nitrogen stable isotope analysis reveals the trophic behavior of Icelandic fin whales in winter and suggests variable feeding strategies. *Mar Mamm Sci* 40:e13097
- Ropert-Coudert Y, Hindell M, Phillips R, Charrassin JB and others (2014) Biogeographic patterns of birds and mammals. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B and others (eds) *Biogeographic atlas of the Southern Ocean*. Scientific Committee on Antarctic Research, Cambridge, p 364–387
- Ruiz-Cooley RI, Koch PL, Fiedler PC, McCarthy MD (2014) Carbon and nitrogen isotopes from top predator amino

- acids reveal rapidly shifting ocean biochemistry in the outer California Current. *PLOS ONE* 9:e110355
- ✦ Sarmiento JL, Slater R, Barber R, Bopp L and others (2004) Response of ocean ecosystems to climate warming. *Global Biogeochem Cycles* 18:GB3003
- ✦ Sergi S, Baudena A, Cotté C, Ardyna M, Blain S, d'Ovidio F (2020) Interaction of the Antarctic Circumpolar Current with seamounts fuels moderate blooms but vast foraging grounds for multiple marine predators. *Front Mar Sci* 7: 416
- ✦ Seyboth E, Botta S, Mendes CRB, Negrete J, Dalla Rosa L, Secchi ER (2018) Isotopic evidence of the effect of warming on the northern Antarctic Peninsula ecosystem. *Deep Sea Res II* 149:218–228
- Sigman DM, Fripiat F (2019) Nitrogen isotopes in the ocean. In: Cochran JK, Bokuniewicz HJ, Yager PL (eds) *Encyclopedia of ocean sciences*, 3rd edn. Academic Press, London, p 263–278
- ✦ Smith S, Altieri KE, Mduyana M, Walker DR and others (2022) Biogeochemical controls on ammonium accumulation in the surface layer of the Southern Ocean. *Biogeochemistry* 19:715–741
- ✦ Soares MA, Bhaskar PV, Naik RK, Dessai D, George J, Tiwari M, Anilkumar N (2015) Latitudinal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variations in particulate organic matter (POM) in surface waters from the Indian Ocean sector of Southern Ocean and the Tropical Indian Ocean in 2012. *Deep Sea Res II* 118:186–196
- ✦ Sokolov S, Rintoul SR (2009) Circumpolar structure and distribution of the Antarctic Circumpolar Current fronts. 1. Mean circumpolar paths. *J Geophys Res* 114:C11018
- ✦ Somes CJ, Schmittner A, Galbraith ED, Lehmann MF and others (2010) Simulating the global distribution of nitrogen isotopes in the ocean. *Glob Biogeochem Cycles* 24: GB4019
- Spieß A (2018) propagate: propagation of uncertainty. R package version 1.0-6. <https://CRAN.R-project.org/package=propagate>
- ✦ St John Glew K, Espinasse B, Hunt BPV, Pakhomov EA and others (2021) Isoscape models of the Southern Ocean: predicting spatial and temporal variability in carbon and nitrogen isotope compositions of particulate organic matter. *Glob Biogeochem Cycles* 35:e2020GB006901
- ✦ Staniland IJ, Gales N, Warren NL, Robinson SL, Goldsworthy SD, Casper RM (2010) Geographical variation in the behaviour of a central place forager: Antarctic fur seals foraging in contrasting environments. *Mar Biol* 157: 2383–2396
- ✦ Staniland IJ, Robinson SL, Silk JRD, Warren N, Trathan PN (2012) Winter distribution and haul-out behaviour of female Antarctic fur seals from South Georgia. *Mar Biol* 159:291–301
- ✦ Stirnimann L, Bornman TG, Forrer HJ, Mirkin J and others (2024) A circum-Antarctic plankton isoscape: carbon export potential across the summertime Southern Ocean. *Glob Biogeochem Cycles* 38:e2023GB007808
- ✦ Tarroux A, Lowther AD, Lydersen C, Kovacs KM (2016) Temporal shift in the isotopic niche of female Antarctic fur seals from Bouvetøya. *Polar Res* 35:31335
- ✦ Thomalla SJ, Nicholson SA, Ryan-Keogh TJ, Smith ME (2023) Widespread changes in Southern Ocean phytoplankton blooms linked to climate drivers. *Nat Clim Change* 13:975–984
- ✦ Trathan PN, Fielding S, Hollyman PR, Murphy EJ, Warwick-Evans V, Collins MA, Link J (2021) Enhancing the ecosystem approach for the fishery for Antarctic krill within the complex, variable, and changing ecosystem at South Georgia. *ICES J Mar Sci* 78:2065–2081
- ✦ Treasure AM, Ruzicka JJ, Moloney CL, Gurney LJ, Anson IJ (2015) Land–sea interactions and consequences for sub-Antarctic marine food webs. *Ecosystems* 18:752–768
- Trueman CN, St John Glew K (2019) Isotopic tracking of marine animal movement. In: Hobson KA, Wassenaar LI (eds) *Tracking animal migration with stable isotopes*, 2nd edn. Elsevier, Academic Press, London, p 137–172
- ✦ Trueman CN, MacKenzie KM, Palmer MR (2012) Identifying migrations in marine fishes through stable-isotope analysis. *J Fish Biol* 81:826–847
- ✦ Vander Zanden MJ, Clayton MK, Moody EK, Solomon CT, Weidel BC (2015) Stable isotope turnover and half-life in animal tissues: a literature synthesis. *PLOS ONE* 10: e0116182
- Walters A (2014) Quantifying the trophic linkages of Antarctic marine predators. PhD dissertation, University of Tasmania, Hobart
- ✦ Walters A, Hindell M, Goebel ME, Bester MN, Trathan PN, Oosthuizen WC, Lea MA (2020) Southern Ocean isoscapes derived from a wide-ranging circumpolar marine predator, the Antarctic fur seal. *Ecol Indic* 118:106694
- ✦ Waluda CM, Collins MA, Black AD, Staniland IJ, Trathan PN (2010) Linking predator and prey behaviour: contrasts between Antarctic fur seals and macaroni penguins at South Georgia. *Mar Biol* 157:99–112
- ✦ Wege M, de Bruyn PJN, Hindell MA, Lea MA, Bester MN (2019) Preferred, small-scale foraging areas of two Southern Ocean fur seal species are not determined by habitat characteristics. *BMC Ecol* 19:36
- ✦ Whiteman J, Elliott Smith E, Besser A, Newsome S (2019) A guide to using compound-specific stable isotope analysis to study the fates of molecules in organisms and ecosystems. *Diversity* 11:8
- ✦ Woods B, Walters A, Hindell M, Trebilco R (2020) Isotopic insights into mesopelagic niche space and energy pathways on the southern Kerguelen Plateau. *Deep Sea Res II* 174:104657
- ✦ Woods BL, Walters A, Hindell M, Revill AT and others (2022) Trophic structure of Southern Ocean squid: a cross-basin analysis of stable isotopes in archived beaks from predator stomachs. *Mar Ecol Prog Ser* 685:137–152
- ✦ Zhu G, Zhang H, Song Q, Yang Y, Wang S, Yang Q (2018) Inferring trophic variation for Antarctic krill (*Euphausia superba*) in the Antarctic Peninsula from the austral fall to early winter using stable isotope analysis. *Acta Oceanol Sin* 37:90–95

Editorial responsibility: Elliott Hazen,
Pacific Grove, California, USA

Reviewed by: K.W. McMahan and 1 anonymous referee

Submitted: February 7, 2024

Accepted: September 5, 2024

Proofs received from author(s): October 12, 2024