No distinct local cuisines among humpback whales: A population diet comparison in the Southern Hemisphere

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HIGHLIGHTS

- Different Southern hemisphere humpback whale populations have distinct fatty acid and stable isotope profiles
- All tested humpback whales are secondary heterotrophs following an omnivorous diet with a diatom origin
- Each tested humpback whale population follows a high-fidelity Antarctic krill diet
- All tested humpback whale populations feed in biologically productive areas

GRAPHICAL ABSTRACT
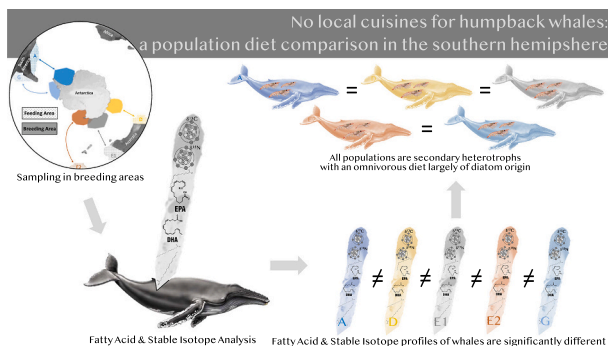
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ABSTRACT

Southern hemisphere humpback whale (*Megaptera novaeangliae*, SHHW) breeding populations follow a high-fidelity Antarctic krill (*Euphausia superba*) diet while feeding in distinct sectors of the Southern Ocean. Their capital breeding life history requires predictable ecosystem productivity to fuel migration and migration-related behaviours. It is therefore postulated that populations feeding in areas subject to the strongest climate change impacts are more likely to show the first signs of a departure from a high-fidelity krill diet. We tested this hypothesis by investigating blubber fatty acid profiles and skin stable isotopes obtained from five SHHW populations in 2019, and comparing them to Antarctic krill stable isotopes sampled in three SHHW feeding areas in the Southern Ocean in 2019. Fatty acid profiles and $\delta^{13}C$ and $\delta^{15}N$ varied significantly among all five populations, however, calculated trophic positions did not (2.7 to 3.1). Similarly, fatty acid ratios, $16:1\omega7c/16:0$ and $20:5\omega3/22:6\omega3$ were above 1, showing that whales from all five populations are secondary heterotrophs following an omnivorous diet with a diatom-origin. Thus, evidence for a potential departure from a high-fidelity Antarctic krill diet was not seen in any population. $\delta^{13}C$ of all populations were similar to $\delta^{13}C$ of krill sampled in productive upwelling areas or the marginal sea-ice zone. Consistency in trophic position and diet origin but significant fatty acid and stable isotope differences demonstrate that the observed variability arises at lower trophic levels. Our results indicate that, at present, there is no evidence of a divergence from a high-fidelity krill diet. Nevertheless, the characteristic isotopic signal of whales feeding in productive upwelling areas, or in the marginal sea-ice zone, implies that future cryosphere reductions could impact their feeding ecology.

1. Introduction

Antarctic krill (*Euphausia superba*; hereafter krill) are a vital part of the Antarctic food web, as most top predators rely either directly or indirectly on them as their food source (Trathan and Hill, 2016). While krill have a circumpolar distribution in the Southern Ocean, an estimated 70 % of their population is concentrated between longitudes 0° and 90°W (Fig. 1; (Nicol and Foster, 2016). Climate change impacts reported for the Antarctic Peninsula region, where the largest concentration of krill has been measured, are not uniform. Nor indeed are they across the entire Southern Ocean (Rogers et al., 2019), leading to strong regional differences in the physical environment and associated biological systems. Inter decadal increases in sea-ice extent have been recorded in the Weddell and Ross Seas while decreases have been
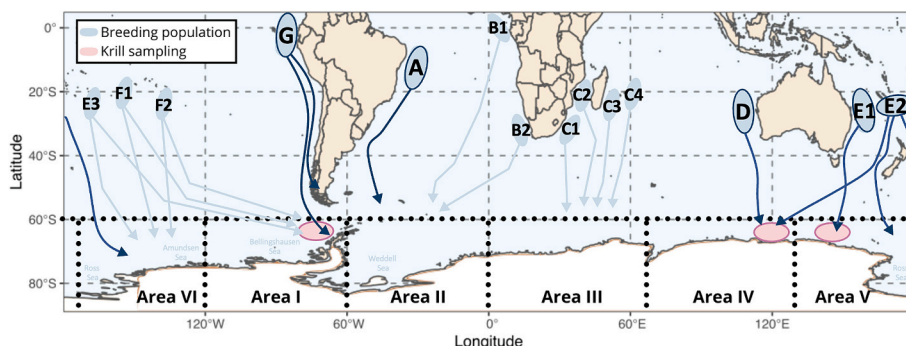

Fig. 1. Map showing the seven humpback whale breeding populations (A – G) recognised by the IWC in the southern hemisphere, and the six IWC management areas (I – VI) in the Southern Ocean. Breeding populations B, C, E, and F are subdivided into sub-populations, which are indicated by numbers. Humpback whale breeding populations and sub-populations are symbolised by light blue ellipses. Dark blue arrows indicate which IWC management area the majority of each of the populations addressed in this study (A, D, E1, E2, G) is thought to utilise as feeding grounds. Light blue arrows indicate where populations not addressed in this study are thought to feed. Antarctic krill sampling locations are indicated by the light pink ellipses. Figure adapted from Acevedo et al. (2013).

recorded in the Bellingshausen and Amundsen Seas, southwest of the West Antarctic Peninsula (WAP; Fig. 1; Parkinson and Cavalieri, 2012), one of the global regions most affected by climate change (Rogers et al., 2019; Turner and Overland, 2009). Phytoplankton blooms have been observed to last longer on the south-eastern side of the WAP and South Orkney Islands region (Barnes, 2015), while bloom duration has decreased on the west side of the WAP (Montes-Hugo et al., 2009). A decline in phytoplankton biomass is predicted along the entire WAP by 2030 (Rogers et al., 2019), which could impact higher trophic level predators such as baleen whales.

Southern hemisphere humpback whales are polar-foraging capital breeders with a high-fidelity krill diet (Chittleborough, 1965; Groß et al., 2020; Waugh et al., 2012). They use stored energy reserves, accumulated through intensive summer feeding, to migrate from their feeding grounds in the Southern Ocean to their breeding grounds at lower latitudes (Chittleborough, 1965). The annual migration is associated with voluntary fasting, intensifying the energetic demands of migration and migration-associated activities like competitive breeding behaviour in males and mating, gestation, parturition, and lactation in females (Dawbin, 1966). The reproductive success and survival of humpback whales are therefore linked to their feeding success in the Southern Ocean (Millar and Hickling, 1990). Inadequate availability of their principal prey item may therefore be mitigated by behavioural changes, such as prolonged stays in Antarctic feeding grounds, supplementary feeding along migration routes, or changes in prey type, or feeding location (Bengtson Nash et al., 2018; Castrillon et al., 2017; Eisenmann et al., 2016; Owen et al., 2017; Pallin et al., 2022; Pirotta et al., 2021).

Recently, long-term monitoring of SHHWs revealed signals of stress in humpback whale ecophysiology that coincided with extreme climatic events in the associated Antarctic feeding grounds (Bengtson Nash et al., 2023, 2018). It is therefore of interest to explore whether populations of SHHW associated with different Antarctic feeding regions show varying indications of dietary plasticity in response to reported varying degrees of climatic pressure. Currently, seven distinct breeding populations of humpback whales (A – G, Fig. 1) are recognised by the International Whaling Commission (IWC) in the southern hemisphere (IWC, 2015). These are associated with six Southern Ocean management areas, I – VI (hereafter "areas"; Fig. 1) where the respective populations feed (Fig. 1).

Potential changes in prey type or feeding location can be assessed through the use of biochemical tracers of diet. A combined approach using fatty acids (FA) and stable isotopes (SI) is commonly used to understand trophic dynamics in the marine environment, as both tracers provide complementary information (Hooker et al., 2001; Ko et al., 2016; Schukat et al., 2014). Each method has strengths and weaknesses, especially when applied in trophic ecology of secondary consumers such as SHHW (Budge et al., 2006; Fry, 2006). Their combined application can mitigate possible weaknesses in the use of one technique alone.

While biochemical dietary investigations have been performed on two (E1, G) of the seven SHHW populations (Bengtson Nash et al., 2018; Bengtson Nash et al., 2023; Eisenmann et al., 2017, 2016; Groß et al., 2020; Haro et al., 2016; Waugh et al., 2012), no study has produced a within-season, inter-population comparison. To the best of our knowledge, this study is the first effort to conduct a temporally aligned circumpolar investigation into the feeding ecology of different SHHW populations, using the above outlined ecological tracers. The study further incorporated parallel comparison to krill sampled in the same year to avoid confounding factors associated with temporal variability (Groß et al., 2020). This within-season geographic comparison of the SHHW diet will add to our current understanding of their feeding ecology and will provide valuable baselines for the detection of change in their high-fidelity krill diet during a time of accelerated climatic change (Purich and Doddridge, 2023).

2. Methods

2.1. Sample collection

Humpback whale blubber and skin biopsies were collected from the A, D, E1, E2, and G populations and sub-populations in August and September 2019 in or near their respective breeding grounds off Brazil (17°52′S, 39°05′W), Western and Eastern Australia (21°55′S, 114°10′E and 27°26′S, 153°34′E, respectively), New Caledonia (22°36′S, 167°00′E) and Colombia (05°36′N, 77°21′W; all coordinates are approximations). Biopsies were either obtained with a crossbow fitted with a specially adapted bolt (Lambertsen, 1987; Palsbøll et al., 1991), or a modified 0.22 calibre rifle (Paxarms™ NZ) and flotation darts (Krützen et al., 2002). All biopsy samples were taken from the whale's dorsum, ventral, and caudal to the dorsal fin as recommended by Lambertsen et al. (1994). Tissue samples were immediately stored on ice in the field, and then transferred to −20 °C freezers for one and a half years until sub-sectioning of the tissue and subsequent analyses. The extended storage of the samples at −20 °C might have led to some degradation, possibly having impacted FA results (Lacombe et al., 2024; Lind et al., 2012; Nieminen et al., 2018). All samples were collected under appropriate state, national, and marine park permits, and tissue biopsy collection was approved by animal ethics committees from institutions in the respective countries.

Krill samples were collected from feeding grounds of three SHHW populations (D, E1, G; Fig. 1) onboard three different vessels between January and March 2019. The fishing vessel *FV Saga Sea* (Aker Bio-Marine Oslo, Norway) obtained samples from area II, around the WAP and the SOI (Fig. 1). The vessel's Eco-Harvesting technique was used to continuously pump krill from a mid-water trawl net onto the vessel. This method ensures that krill remains intact. A daily random sample of 20 individual krill was taken from the catch, divided into two foil or vacuum-sealed packs, and frozen immediately aboard the vessel at −20 °C for 4 h. Afterwards samples were stored at −80 °C until they were transported on dry ice to Hobart, Australia, where they were stored in a −20 °C freezer for two years until analysis. Krill samples in area IV were collected on board the research vessel *Umitaka-maru* (Tokyo University of Marine Science and Technology, Japan; Fig. 1). Krill was only encountered at one station along 110°E and collected using a Matsuda-Oozeki-Hu trawl (MOHT; Oozeki et al., 2004) open/close frame net. Samples were frozen in liquid nitrogen and stored on board at −60 °C before being transferred to a −80 °C freezer in Tokyo, Japan until analysis. Krill samples in area V were collected on board the research vessel *Investigator* (Marine National Facility, Australia; Fig. 1) during the multi-disciplinary marine science voyage "ENRICH" (Euphausiids and Nutrient Recycling in Cetacean Hotspots) during January and March 2019 (Miller et al., 2019). Target trawls were undertaken using a rectangular midwater trawl net (RMT8) with a mesh size of 4.5 mm (Baker and Clarke, 1973), and by aiming for dense marks or scattering layers observed on the echosounder. Immediately after sampling, up to 100 krill in good condition were snap frozen in liquid nitrogen and stored in a −86 °C freezer until analysis.

2.2. Lipid extraction

A modified (Bligh and Dyer, 1959) methanol-dichloromethane-water (MeOH/DCM/H$_2$O) method (2:1:0.8 v/v/v) was used to extract lipids overnight from pre-weighed (ca. 0.03 g) blubber samples, as previously described (Waugh et al., 2012). Following phase separation through the addition of 10 ml DCM and 10 ml saline Milli-Q H$_2$O solution, the lower layer, containing the total lipid extract, was drained and dried using rotary evaporation. DCM was added to the remaining lipid extract, which was transferred to a pre-weighed glass vial and further dried under a stream of nitrogen gas. The total lipid content, expressed as percent lipid of the initial blubber sample, was quantified by weighing the dried lipid extract.

2.3. Fatty acids

Specific polyunsaturated FA (PUFA), called trophic markers, can mainly be synthesised by primary producers and, hence, are used to determine carbon and food source preferences (Budge et al., 2006). The turnover rate of FA is relatively fast in marine mammals, hence dietary shifts are estimated to be observable in whale blubber after one month (Budge et al., 2006). Ratios of FA can be used to interpret feeding strategies such as herbivory versus carnivory (Auel et al., 2002; Falk-Petersen et al., 1990). However, some saturated (SFA) and mono-unsaturated FA (MUFA) can be elongated or desaturated during the metabolic process, making interpretation of the specific origin difficult (Budge et al., 2006; Cook, 1991). Nevertheless, these metabolic changes are often inhibited during fasting or consumption of a high-fat diet like krill (Budge et al., 2006).

2.3.1. Fatty acid determination

An aliquot of the total blubber lipid extract was *trans*-methylated with 3 ml MeOH/HCl/DCM (10:1:1 v/v/v) to produce fatty acid methyl esters (FAME), as described in detail in (Groß et al., 2020). Briefly, the mixtures were heated for 1 h at 100 °C. Subsequently, 1 ml of H_2O and 1.5 ml hexane/DCM (4:1 C_6/DCM v/v) were added to the aliquot, with the phases being separated by centrifugation (5 min at 2000 rpm) and the top layer extracted to a glass vial. This step was repeated three times. An internal injection standard (23:0) was added before analysing FAME extracts with a gas chromatograph (Agilent Technologies 7890A) equipped with a Supelco Equity™-1 fused silica capillary column (15 m × 0.1 mm internal diameter, 0.1 μm film thickness) (Alhazzaa et al., 2011). FAME identifications were confirmed by analysing representative samples on a Finnigan Thermoquest GCQ gas chromatograph-mass spectrometer fitted with a column of similar polarity as used in the gas chromatograph and an on-column injector. Individual FA are expressed as percent of the total FA (TFA).

2.3.2. Fatty acid calculations

According to the FA trophic biomarker concept, specific FA and ratios of FA can be used as indicators for diet sources (Dalsgaard et al., 2003). Palmitoleic acid (16:1ω7c) and eicosapentaenoic acid (EPA; 20:5ω3) are indicative of a diatom-origin diet, while AA (18:4ω3) and docosahexaenoic acid (DHA; 22:6ω3) are indicative of a dinoflagellate-origin diet. The ratios of palmitoleic acid to palmitic acid (16:1ω7c/16:0) and EPA/DHA are also used as indexes of diatom-origin diets (Dalsgaard et al., 2003). The ratio of vaccenic acid to oleic acid (18:1ω7c/18:1ω9c) and PUFA to SFA are known carnivory biomarkers. In addition, the modified carnivory index (CI), which is based on (Schukat et al., 2014) and divides oleic acid (18:1ω9c) by the sum of all herbivorous biomarkers and 18:1ω9c, was used and calculated as follows:

$$CI = \frac{18:1\omega9c}{(16:1\omega7c + 16:4\omega1 + 18:1\omega7c + 18:4\omega3 + 18:1\omega9c)}$$

Compared to the original index, the modified CI ranges from 0 for herbivorous to 1 for carnivorous feeding (Bode et al., 2015).

2.4. Stable isotopes

Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios are used to determine food sources and trophic positions, respectively. $\delta^{13}C$ of primary producers is conserved through the food web (McConnaughey and McRoy, 1979), while $\delta^{15}N$ increases with each trophic level (~3.4 ‰; Minagawa and Wada, 1984). Ecological applications of SI require careful consideration because they can vary spatially and temporally at the base of the food web and are, therefore, not always indicative of a specific diet (Fry, 2006; Goericke and Fry, 1994). Thus far, isotopic turnover time has only been determined for bottlenose dolphins (*Tursiops truncatus*), at 104 days for $\delta^{13}C$ and 180 days for $\delta^{15}N$ (Browning et al., 2014). Considering that humpback whales are phylogenetically closely related to bottlenose dolphins, we assume that a similar time frame of 104–180 days is applicable.

2.4.1. Stable isotope analysis

Non-lipid extracted SHHW skin tissue was oven dried overnight at 58 °C and non-lipid extracted whole krill individuals from areas II and V were freeze dried at −50 °C for 48 h. Tin capsules were filled with 1–2 mg of powdered SHHW skin and 0.45–0.55 mg of powdered krill. Humpback whale samples were analysed at the Stable Isotope Laboratory at Griffith University using a Europa EA-GSL, interfaced to a SERCON Hydra 20–20 isotope ratio mass-spectrometer. International standards IAEA-CH-6 for carbon and IAEA N1 for nitrogen were used to calibrate laboratory standards sucrose and $(NH_4)_2SO_4$. Based on replicate standards, the mean standard deviation for $\delta^{13}C$ and $\delta^{15}N$ was 0.2 ‰ and 0.1 ‰, respectively. Antarctic krill samples from areas II and V were analysed at the Central Science Laboratory at the University of Tasmania using a varioPYRO cube coupled to an Isoprime 100 mass spectrometer for flash combustion. International reference standards with known isotopic composition (USGS 25, USGS 40, USGS 41, IAEA-N1 and IAEA-N2, NBS 21, USGS24) were used to correct for instrumental drift and quality assurance purposes, which resulted in mean standard deviations of 0.1 ‰ for both isotopes. Antarctic krill samples from area IV were analysed at the Atmosphere and Ocean Research Institute at the University of Tokyo. Prior to SI analysis, lipids were extracted using a methanol-chloroform mixture (1:2 *v/v*) for 24 h. Krill samples were then washed twice with methanol before being oven-dried at 60 °C for 24 h prior to analysis using a Flash 2000 – ConFlo IV – IRMS (Delta V). L-Alanine was used as a standard and analytical instrument precision was 0.2 ‰ and 0.1 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Carbon and nitrogen weights as well as isotope values were generated, and atomic C:N ratios were calculated. The following formula was used to calculate SI abundances in units of permil (‰), where X = ^{13}C or ^{15}N and R = the respective ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$:

$$\delta X = \left[\left(\frac{Rsample}{Rstandard} \right) - 1 \right] \times 1000$$

Non-lipid extracted SHHW skin samples were lipid-corrected using the following two-source mass balance mixing equation proposed by (Fry, 2002):

$$\delta^{13}C_{LF} = \delta^{13}C + D - \left(\frac{D \times C:N_{LF}}{C:N} \right)$$

where $\delta^{13}C_{LF}$ = lipid corrected $\delta^{13}C$, D = protein-lipid discrimination factor and $C:N_{LF}$ = theoretical lipid-extracted C:N ratio. The values for D and $C:N_{LF}$, 8.92 and 3.1, respectively, were determined for E1 skin tissue by (Groß et al., 2021).

Non-lipid extracted Antarctic krill samples were lipid corrected using the following krill-specific model for euphausiid species developed by (Logan et al., 2008):

$$\delta^{13}C_{LF} = \delta^{13}C + 6.941 - \left(\frac{6.941 \times 3.346}{C} : N \right)$$

Population-specific trophic positions were calculated from feeding ground-specific $\delta^{15}N_{base}$ (based on krill $\delta^{15}N$ from management areas where the majority of each humpback whale population is thought to feed) as follows:

$$Trophic\ position = \lambda + \left(\delta^{15}N_{consumer} - \delta^{15}N_{base} \right) / \Delta_n$$

where λ = trophic position of the organisms used to estimate $\delta^{15}N_{base}$ and Δ_n = enrichment of $\delta^{15}N$ per trophic level. Here, we used λ = 2 for Antarctic krill (Schmidt et al., 2006) and an enrichment of Δ_n = 3.4 ‰ (Minagawa and Wada, 1984; Post, 2002). Trophic position results are reported as population-specific mean ± standard error.

Humpback whale $\delta^{15}N$ ($\delta^{15}N_{HW}$) were baseline-corrected ($\delta^{15}N_{Bc}$) using mean $\delta^{15}N$ of krill ($\delta^{15}N_{AK}$) sampled in the putative or adjacent feeding grounds of each population if krill values for a feeding ground were unavailable. Baseline correction using zooplankton SI values was recommended by Yang et al. (2021) in a circumpolar Southern Ocean study of *E. superba* isoscapes. $\delta^{15}N_{HW}$ of populations A and G, D, and E1 and E2 were baseline-corrected using $\delta^{15}N_{AK}$ of areas II, IV, and V, respectively. Baseline corrections were calculated as follows:

$$\delta^{15}N_{Bc} = \delta^{15}N_{HW} - \delta^{15}N_{AK}$$

2.5. Data analysis

Lipid, FA, and SI data were analysed (separately and jointly) in PRIMER v7 (Clarke and Gorley, 2015) with PERMANOVA+ add-on (Anderson et al., 2008; http://www.primer-e.com) and R (version 3.5.3). A significance level of $\alpha = 0.05$ was used for the interpretation of all results and all mean FA and SI values are reported with standard error. Homoscedasticity and normality were tested for all data using Levene's test and a Shapiro-Wilk test in R, respectively. Homogeneity of dispersion for multivariate data was tested using the PermDisp routine in PRIMER. No groups followed a normal distribution and homogeneity of variances, but group dispersions were not significantly different.

2.5.1. Fatty acids

Prior to calculating Euclidean distance matrices for all multivariate analyses, all FA data were square root transformed to reduce the influence of FA that had large percentages. FAs present at <0.5 % were combined and included as "Others" in the statistical treatment of the results (listed in Table S1). Differences and similarities in FA profiles (defined as the percentage distribution of all FA present) among populations and sub-populations were visualised using a principal component analysis (PCA) generated in R. The PCA was also used to identify those fatty acids that explain most of the variability in the data set. Statistical differences in total lipid content, FA profiles, and SI among populations (fixed factor) were tested using a one-factor permutational multivariate ANOVA (PERMANOVA) in PRIMER with subsequent post-hoc pairwise analysis. Subsequently, a canonical analysis of principal coordinates (CAP) in PRIMER was used to assess how distinct the populations are from one another based on FA profiles and SI.

2.5.2. Stable isotopes

Statistical differences in $\delta^{13}C$ and $\delta^{15}N$ among populations and sub-populations (fixed factor) were tested using a one-factor PERMANOVA in PRIMER. Distinction among populations in $\delta^{13}C$ and $\delta^{15}N$ was assessed using the CAP analysis in PRIMER.

2.5.3. Fatty acids and stable isotopes results combined

Stable isotope and combined datasets of FA and SI were normalised by subtracting the mean and dividing by the standard deviation to put them all on comparable measurement scales. For SI and combined datasets, one-factor analysis of similarity (ANOSIM) in PRIMER was used to examine biochemical tracer similarities within and among populations and a global R statistic was calculated, which is a scaled measure of separation between groups of samples. Relative global R values close to 0 indicate no difference while values close to 1 are very different. The similarity percentages (SIMPER) routine in PRIMER was then used to examine which biochemical tracer contributed to the separation of populations. To test the relationship between similarity matrices of FA and SI, a RELATE routine in PRIMER was used to determine the degree to which among-sample similarities agreed for both biochemical tracers.

3. Results

3.1. Fatty acids

Overall, 54 different FA were identified in SHHW blubber samples. Of these, 15 were present in quantities greater than trace amounts (≥ 0.5 % TFA) and accounted for around 95 % of TFA in each population (Table S1). The five most abundant FA, which accounted for approximately 65–70 % of TFA, were (in decreasing order of relative abundance): 18:1ω9c, 16:1ω7c, 16:0, 18:1ω7c and 14:0 (Table S1). A PCA including these 15 major FA showed that 60 % of the variability in FA profiles was explained by PC1 and PC2, but the different populations did not form distinct clusters (Fig. 2). The FA that contributed most to the spread in the PCA were two SFA, 14:0 and 16:0, two MUFA, 14:1 and a diatom FA trophic marker, 16:1ω7c, and an indicator FA for both diatoms and krill, 20:5ω3 (Fig. 2). A one-factor PERMANOVA showed that the FA profiles of all five populations were significantly different from each other (PERMANOVA: pseudo-$F_{4,118} = 9.2892$, $p = 0.0001$). A post-hoc pairwise PERMANOVA showed that the FA profiles of all populations, except A and D, varied significantly from each other, with global R values ranging from 0.13 to 0.49 (Table S2).

As the scores of individual whale samples from each population did not form distinct clusters in the PCA, but PERMANOVA results indicated statistically significant differences between the populations, a CAP analysis was performed. The CAP supported the PERMANOVA results and showed clear clustering of samples. Population G formed its own group and had higher relative levels of omega-3 and long-chain (LC $\geq C_{20}$) PUFA compared to all other populations (Fig. 3, Table S1). Populations A and D formed two separate, but close together clusters (Fig. 3). The FA profiles of these two populations were similar with nearly equal percentages of SFA, MUFA, LC-PUFA and omega-3 PUFA (Table S1). Sub-populations E1 and E2 formed two overlapping clusters and compared to the FA profiles of populations A and D, both sub-populations had higher SFA levels and lower short-chain MUFA levels (Fig. 3, Table S1). Overall, 80 % of samples ($n = 123$) were correctly classified to the population from which they originated by the CAP cross validation procedure (Table S3). There was a classification success of 83, 87, 72, 68, and 80 % for the A, D, E1, E2, and G populations, respectively (Table S3).

3.2. Stable isotopes

There was a statistically significant difference in $\delta^{13}C$ and $\delta^{15}N$ between all populations (PERMANOVA: pseudo-$F_{4, 118} = 20.07$, $p < 0.001$), except between sub-populations E1 and E2. A post-hoc pairwise comparison showed that global R values ranged from 0.1 to 0.6 for all pairwise comparisons (Table S2). Population D had the lowest mean $\delta^{13}C$ (-25.5 ± 0.1 ‰) and population A had the highest (-23.8 ± 0.2 ‰; Fig. 4). Population E1 had the lowest mean $\delta^{15}N$ (6.8 ± 0.1 ‰), while population G had the highest (7.5 ± 0.1 ‰; Fig. 4). A SIMPER analysis showed that within population differences for A, E2, and G were mainly explained by $\delta^{13}C$ variability, while within population differences for D and E1 were equally explained by both isotopes (Table S4). All inter-population differences were driven by variability in $\delta^{13}C$, except between E1 and E2 (Table S4).

Mean $\delta^{13}C$ of all five SHHW populations were similar to mean $\delta^{13}C$ of krill sampled in areas II and IV, but were significantly higher than mean $\delta^{13}C$ of krill sampled in area V (Fig. 4). Using mean $\delta^{15}N$ of krill collected in the putative or adjacent feeding grounds of each population, the mean $\delta^{15}N$ enrichment between SHHW and krill in 2019 ranged from 2.6 ‰ for population D to 3.8 ‰ in sub-population E2 (Fig. 4, Table S5). Population A had the lowest mean trophic position of 2.7 ± 0.1, and sub-population E2 the highest position of 3.1 ± 0.2 (Table S1). The ANOSIM showed that all populations had statistically significant differences in trophic position, except for population pairs D/G and E1/E2.
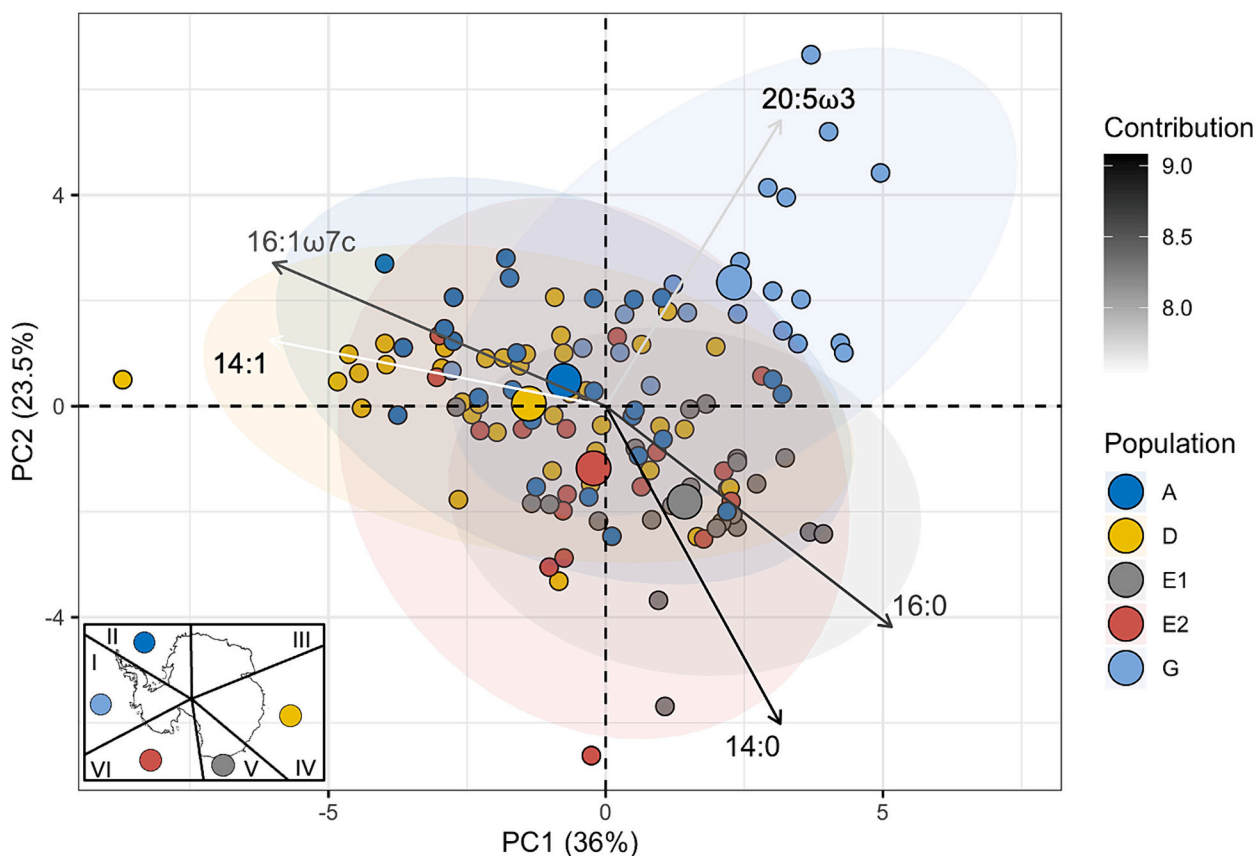
Fig. 2. Principal component analysis (PCA) biplot of blubber (B) fatty acid profiles of A, D, E1, E2 and G (B = 26, 39, 22, 18, 20; sampled off Brazil, west Australia, east Australia, New Caledonia and Colombia in 2019, respectively) humpback whale populations showing both PCA scores for individuals and loadings for variables. The colour gradient of arrows shows the PCA loadings of each specified fatty acid. The larger data point in each population cluster represents the mean of each population. The map insert on the bottom left shows the IWC management areas (denoted by Roman numerals I-VI) in which each population (denoted with coloured circles) is thought to feed during the austral summer.
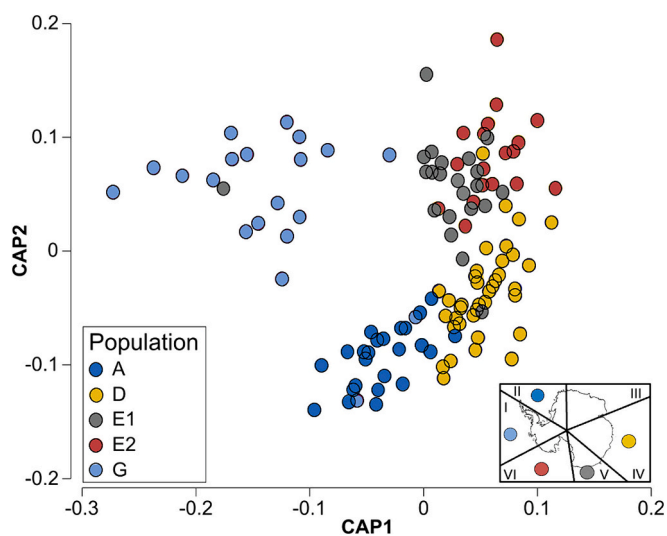

Fig. 3. Canonical analysis of principal coordinates (CAP) of blubber (B) fatty acid profiles of A, D, E1, E2 and G (B = 26, 39, 22, 18, 20; sampled off Brazil, west Australia, east Australia, New Caledonia and Colombia in 2019, respectively) humpback whales. The map insert on the bottom right shows the IWC management areas (denoted by Roman numerals I-VI) in which each population (denoted with coloured circles) is thought to feed during the austral summer.
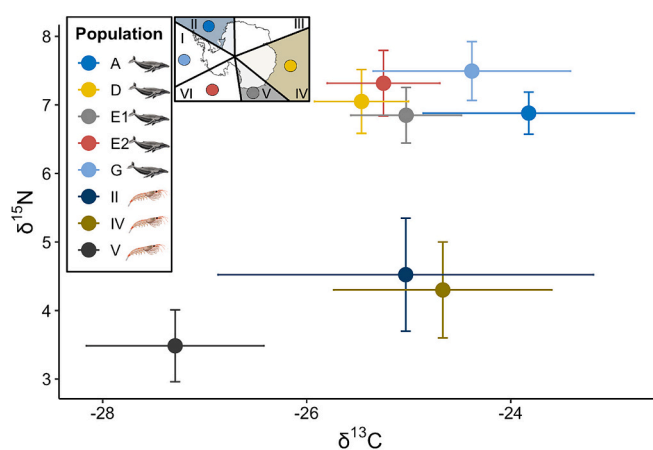

Fig. 4. Biplot showing the mean and standard deviation of skin (S) $\delta^{13}C$ and $\delta^{15}N$ of A, D, E1, E2 and G (S = 30, 40, 21, 26, 27; sampled off Brazil, west Australia, east Australia, New Caledonia and Colombia in 2019, respectively) humpback whale populations and $\delta^{13}C$ and $\delta^{15}N$ of whole krill caught in IWC management areas II, IV and V (n = 36, 8, 3, respectively). IWC management areas (denoted by Roman numerals I-VI) where krill samples were caught are shown as shaded areas in the map insert, which also indicates the areas in which each population (denoted with coloured circles) is thought to feed during the austral summer.

3.3. Fatty acids and stable isotopes results combined

Both biochemical tracers showed significant differences between populations (Table S1). The separation of populations was clearer when using FA profiles alone, which is evident by the reduction of the overall CAP cross validation success from 80 % to 76 % (Table S6) when both biochemical tracers were combined into one dataset with 17 variables. This is probably due to the fact that there are 15 major FA in the analyses, but only two different SI. A RELATE analysis comparing the FA and SI Euclidean distance matrices found that the relative differences among populations were correlated ($p = 0.01$) and that this relationship was strong ($\rho = 0.9$). This shows that FA and SI provide similar results for among sample relationships. The SIMPER analysis showed that there was no consistent pattern of FA or SI explaining within or among population differences. Nevertheless, 20:1ω9c, a calanoid copepod biomarker, contributed 22 % to the mean squared difference within population E2 and also to most of the mean squared differences between this and all other populations (Table S6). The PUFAs, 20:5ω3 and 18:4ω3, contributed most to the mean squared differences between population G and all other populations (Table S6). Plotting FA ratios against δ^{15}N showed that the enrichment of ^{15}N is not consistent among all FA ratios used as indicators of carnivorous feeding (Fig. 5). Although the E1 sub-population had the highest modified CI, the D population had the highest 18:1ω7c/18:1ω9c ratio (original CI) and the G population had the highest ^{15}N enrichment (Fig. 5). Only the ratio of PUFA/SFA aligned with the enrichment of ^{15}N. All five populations had ratios of 16:1ω7c/16:0 and 20:5ω3/22:6ω3 above 1, which indicates that a significant portion of the diet had a diatom-origin. Population D had the highest 16:1ω7c/16:0 ratio, 1.9 ± 0.1, while population A had the highest 20:5ω3/22:6ω3 ratio, 1.7 ± 0.1 (Table S1).

4. Discussion

The within-season diet comparison of five distinct SHHW populations and sub-populations, and the results presented herein allow for inferences about the spatial variability in the SHHW feeding locations and diet sources. Our results show that both FA profiles and SI differ significantly among all five populations. Both biochemical tracers show a pronounced distinction between populations A, D and G. SI values were not as distinctive between sub-populations E1 and E2 as these were from the other three populations. Despite these significant differences, FA ratios suggested that all five populations followed an omnivorous

diet with a diatom-based food web, supporting δ^{15}N results that indicated that all five populations are secondary heterotrophs feeding at trophic positions of 2.7 to 3.1. Combined, results from both lines of evidence suggest that the observed variability arises at lower trophic levels, as previously concluded for observed within-population temporal variability for the E1 stock (Groß et al., 2020). Therefore, despite differing reported rates and degree of climatic perturbation around the circum-Antarctic region, these do not appear to have led to a departure from a high-fidelity krill diet in any population during the 2018/2019 austral summer preceding sampling. Notably, δ^{13}C of each population was not similar to δ^{13}C of krill sampled in the putative or adjacent feeding grounds of each population. δ^{13}C of all five populations correspond to δ^{13}C found in biologically productive areas influenced by upwelling, or in the marginal sea-ice zone (Graham et al., 2010). This observation clearly indicates that the whales preferentially use these areas for feeding. This signal may have overshadowed any spatial alignment of δ^{13}C of whales and krill from the same IWC management area.

Results from the FA and SI analyses show that all five populations consumed an omnivorous diet in the austral summer of 2018/2019. SHHW from all five populations fed on low trophic level prey and species with a high diatom-linked diet. These results are indicative of a predator-prey relationship between SHHW and krill, as *E. superba* consume a high diatom diet. Other potential prey species of SHHW in the Southern Ocean, *Thysanoessa macrura* and *Munida gregaria*, are known to consume more dinoflagellates (Raymond et al., 2011). Feeding on these other species would reduce the whales' EPA to DHA ratio, which was not observed in this study. Feeding on higher trophic levels would increase the whales' CI as well as decrease the ratio of 18:1ω7c/18:1ω9c and increase the ratio of PUFA/SFA to indicate more carnivorous than omnivorous feeding.

A predator-prey relationship between SHHW and krill is corroborated by the mean calculated trophic position of 2.9. It shows that SHHW of all five populations are secondary consumers (trophic position 2.0 to 3.0), feeding on the third trophic level in the Antarctic food web, as expected under the classical feeding paradigm. Additionally, the mean diet-tissue discrimination between krill and SHHW in this study was 3.2 ‰, which aligns closely with the literature mean of 3.4 ‰ per trophic level (Minagawa and Wada, 1984). There was, however, only a mean δ^{15}N difference of 1.5 ‰ among populations which, while significant, does not equate to feeding on different trophic levels. If SHHW were feeding on a higher trophic level than krill, their δ^{15}N would likely
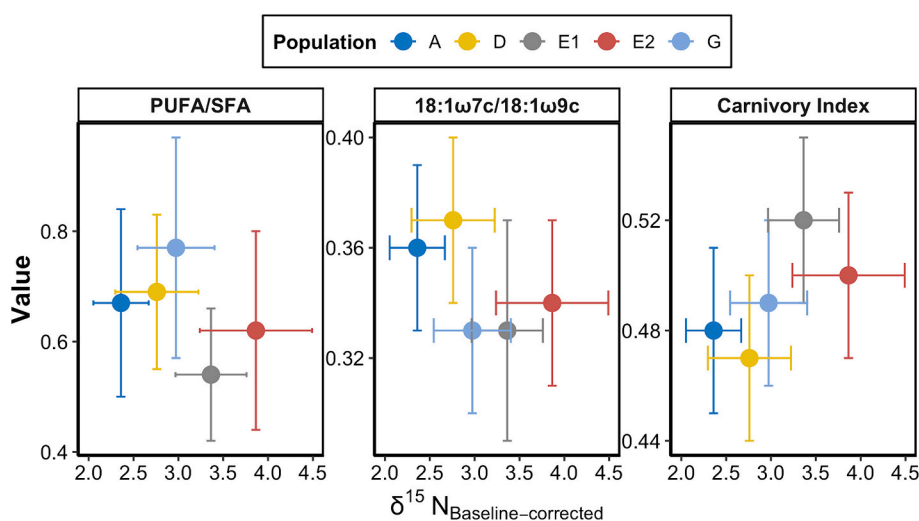

Fig. 5. Plots showing the mean and standard deviation relationship between the ratio PUFA/SFA (left graph), the ratio 18:1ω7c/18:1ω9c (middle graph), and the modified carnivory index (right graph), and δ^{15}N of humpback whale populations A, D, E1, E2 and G ($n = 26, 39, 22, 18, 20$; sampled off Brazil, west Australia, east Australia, New Caledonia and Colombia in 2019, respectively). "n" corresponds to the number of blubber and skin samples used in this analysis.

average 10.3 ‰ rather than the 7.1 ‰ found in this study using the mean diet-tissue discrimination of 3.2 ‰ (Table S1). When baseline-corrected using $\delta^{15}N$ of krill sampled in the putative or adjacent feeding grounds of each population in the austral summer preceding SHHW biopsy collection, population A showed the lowest mean $\delta^{15}N$ and sub-population E2 the highest. These differences in mean $\delta^{15}N$ among populations may have been caused by a higher consumption of juvenile krill, which have lower $\delta^{15}N$ than mature krill (Zhu et al., 2018). Alternatively, $\delta^{15}N$ variability of 1.5 ‰ could also arise from baseline variations not captured here by using $\delta^{15}N$ of a primary consumer, *E. superba*, for baseline corrections rather than $\delta^{15}N$ of phytoplankton or particulate organic matter (Minagawa and Wada, 1984).

The clear statistical separation of SHHW population G from all other populations based on fatty acids is plausible considering that the South Scotia Ridge biogeographically separates their putative feeding grounds of Bransfield and Gerlache Straits as well as Marguerite Bay in area I at 40°W (Friedlaender et al., 2021, 2006; Weinstein and Friedlaender, 2017), from feeding grounds of population A to the east in area II (Dalla Rosa et al., 2008; Engel and Martin, 2009). Thus far, there has been no evidence that whales from population A feed around the SOI, or that whales feeding in the WAP region migrate to the south Atlantic (Engel and Martin, 2009; Stevick et al., 2004). Based on mitochondrial DNA results, whales feeding on the western side of the WAP (populations F and G) are highly differentiated from whales feeding in other Southern Ocean regions, likely due to high site fidelity (Amaral et al., 2016). This is hypothesised to be driven by the high biological productivity and consistent availability of krill around the WAP (Dalla Rosa et al., 2008).

Surprisingly, the A and D populations showed a high degree of similarity in fatty acid profiles despite the geographical distance between their putative feeding grounds (Engel and Martin, 2009; Murase et al., 2002). The close clustering of populations A and D based on FA profiles might be geographically explained by the eastward flow of the Antarctic Circumpolar Current (ACC). The WAP region is hypothesised to serve as a source of krill to the Scotia Sea and beyond (Siegel and Watkins, 2016; Tarling et al., 2007; Thorpe et al., 2004), with krill being transported clockwise around Antarctica by the ACC. The putative feeding grounds of populations A and D are closer to this source region than the feeding grounds of sub-populations E1 and E2, which might explain why FA profiles of A and D are more similar to each other than to E1 and E2.

Sub-populations E1 and E2 demonstrated contradicting ecological tracer findings. While fatty acid profiles were significantly different from each other, $\delta^{13}C$ and $\delta^{15}N$ of both SHHW sub-populations were not significantly different from each other. One possible explanation for this may be a higher degree of fluidity in their feeding ground use, which has been evidenced by satellite tagging and genomic data (Derville et al., 2020; Riekkola et al., 2018; Steel et al., 2018). This is supported by our CAP cross-validation results which showed that 32 % of E2 samples were assigned to SHHW populations E1 or D. Alternatively, our results could be explained by krill swarms traveling across broad spatial scales with the flow of the ACC from area IV through areas V and VI (Siegel and Watkins, 2016), and D, E1 and E2 whales potentially having fed on the same krill swarms in different geographical areas.

$\delta^{13}C$ of all five humpback whale populations were similar to $\delta^{13}C$ of krill sampled in areas II and IV in 2019. This is surprising as efforts were made to match krill collected in the putative feeding grounds of the respective populations in anticipation of a more accurate calculation of trophic enrichment. Assuming an enrichment factor of 0.9 ‰ in $\delta^{13}C$ per trophic level (DeNiro and Epstein, 1978), $\delta^{13}C$ of each population's diet should range from −26.4 to −24.7 ‰, which is only the case for krill sampled in areas II and IV (Fig. 4). $\delta^{13}C$ of krill sampled in area V are much lower, ranging from −29.5 to −26.8 ‰ (Fig. 4). Higher $\delta^{13}C$ of krill sampled in areas II and IV are characteristic of highly productive areas, either being nearshore, close to the marginal sea-ice zone, or influenced by upwelling (Fry and Wainright, 1991; Graham et al., 2010; Magozzi et al., 2017). In area II, Drake Passage and the southern Scotia

Sea, iron-poor warmer waters of the ACC mix with upwelling and horizontally transported iron-rich waters on the shelf (Zhou et al., 2010). $\delta^{13}C$ are higher in these areas compared to open ocean regions because phytoplankton preferentially take up ^{12}C during photosynthesis, increasing $\delta^{13}C$ of aqueous CO_2 by a few parts per thousand as they draw down its concentration during blooms (Graham et al., 2010). This indicates that all five SHHW populations feed in highly productive parts of their feeding areas and that this signal is much stronger than the $\delta^{13}C$ signal of each putative feeding ground.

Our results for SHHW populations feeding in highly productive areas align with previous knowledge from the whaling era as well as current knowledge. During the whaling era, SHHWs were found feeding on shelves around oceanic islands in subpolar latitudes (Mackintosh, 1965). Current knowledge also shows that SHHW are present in biologically rich areas, such as upwelling areas, nearshore embayments and close to the sea-ice edge (Albertson et al., 2018; Andrews-Goff et al., 2018; El-Gabbas et al., 2021; Friedlaender et al., 2021, 2006; Murase et al., 2002; Nowacek et al., 2011; Riekkola et al., 2019; Van Opzeeland and Hillebrand, 2020). For example, local upwelling of Upper Circumpolar Deep Water in the WAP region enhances primary productivity (Prézelin et al., 2004), which leads to high densities of krill and, consequently, high numbers of SHHW from populations G and F (Friedlaender et al., 2006). Several studies found that SHHW from different populations (B, E1, E2, E3, G) move further south throughout the austral summer, following the receding sea-ice edge (Andrews-Goff et al., 2018; El-Gabbas et al., 2021; Riekkola et al., 2019; Van Opzeeland and Hillebrand, 2020). The ice break-up increases light availability, releases nutrients, and seeds the ocean with pelagic phytoplankton, which fosters a highly productive marginal sea-ice edge zone (Van Opzeeland and Hillebrand, 2020). Findings based on acoustic data, model suggestions, and tagging work also show that SHHW are present in open ocean areas. However, our results suggest that SHHW presence is not necessarily an indicator for model-derived suitable feeding habitat as none of the whales in our study had $\delta^{13}C$ consistent with open ocean feeding.

Even though the overall results of the FA and SI analyses led to similar conclusions, and results complemented each other, there was a mismatch between some of the indices. This was especially noticeable when comparing the FA ratios used as indices of carnivory with each other and in relation to ^{15}N enrichment. The varying results between the modified CI and the ratio PUFA/SFA could arise from the latter being more commonly applied to primary consumers such as copepods, amphipods or krill (Hagen et al., 2007; Nyssen et al., 2005). The difference in results between some indices could have led to a reduction in the CAP cross validation success when SI results were added to the 15 FA used in the initial CAP analysis. Alternatively, the set-up of the statistical analyses is based on dissimilarities rather than similarities. The use of FA profiles comprised of 15 major FA may highlight dissimilarities among populations more than the two SI values. This could lead to more similarities in the CAP analysis, resulting in a reduced classification success with 17 variables. These discrepancies between results obtained from the two biochemical tracers, as well as the incongruities between results derived from modelling and tagging studies and our study highlight the importance of using multidisciplinary approaches to address large-scale ecological questions.

Interestingly, the overall CAP cross validation success of fatty acid profiles in this spatial comparison of five SHHW populations was only 1 % higher than the overall CAP cross validation success of FA profiles in a temporal comparison of the E1 sub-population across a 10-year timeline. This is indicative of temporal diet variability within a population being as pronounced as spatial diet variability among populations. This reiterates the point made by Groß et al. (2020) that temporal variability has to be taken into account when assessing trends of changes in the feeding ecology of SHHW. It is imperative to consider both interannual and spatial variability when assessing long-term trends in the feeding ecology of SHHW populations to be able to detect future climate change impacts. The results provided in this manuscript suggest that decreasing

sea-ice extent and warming sea surface temperatures in the Amundsen and Bellingshausen Seas are currently not reflected in the diet of SHHW, as no departure from a high-fidelity krill diet was detected. Expected higher trophic level feeding in G population whales was not evidenced through FA and SI results. Our results indicate that all five populations are secondary consumers, feeding at a similar trophic level, regardless of the climatic conditions in their putative feeding grounds.

5. Conclusion

The high degree of variability in FA profiles and SI values observed among the five SHHW populations was expected, as the majority of each population is thought to feed in different Southern Ocean areas. Within season FA profiles of each population are sufficient to distinguish the five SHHW populations from each other. However, the overall results suggest that each population follows a high-fidelity Antarctic krill diet, which can be used as baseline knowledge to assess the relative extent of climate change impacts reported in the putative feeding grounds in future studies. These results suggest that the observed variability in humpback whale FA profiles and SI arises at lower trophic levels, which supports the findings by Groß et al. (2020).

Based on δ^{13}C of SHHW and krill sampled in 2019, our findings indicate that all five populations are feeding in biologically productive areas either influenced by upwelling or occurring in the marginal sea-ice zone. Feeding in the marginal sea-ice zone or in upwelling areas aligns with results from studies based on satellite tag and modelling data. Although our results of feeding in highly productive areas align with previous research, they are limited by a lack of Antarctic krill sampled in areas II and VI. Future studies would benefit from the inclusion of krill samples from all feeding areas of SHHW. Further monitoring of the feeding ecology of all SHHW populations in both breeding and feeding grounds is strongly suggested, especially using multi-disciplinary approaches as different methods can yield complimentary results. The signal of whales feeding in the marginal sea-ice zone or in upwelling areas implies that future reductions in sea-ice extent and duration, and rising ocean temperatures could impact their feeding ecology.

CRediT authorship contribution statement

Jasmin Groß: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Rita M. Franco-Santos:** Writing – review & editing, Methodology, Formal analysis. **Patti Virtue:** Writing – review & editing, Supervision, Methodology, Formal analysis. **Peter D. Nichols:** Writing – review & editing, Supervision, Methodology, Formal analysis. **John Totterdell:** Writing – review & editing, Methodology, Data curation. **Milton C.C. Marcondes:** Writing – review & editing, Methodology, Data curation. **Claire Garrigue:** Writing – review & editing, Methodology, Data curation. **Natalia Botero-Acosta:** Writing – review & editing, Data curation. **Fredrik Christiansen:** Writing – review & editing, Data curation. **Juliana Castrillon:** Writing – review & editing, Data curation. **Susana J. Caballero:** Writing – review & editing, Methodology, Data curation. **Ari S. Friedlaender:** Writing – review & editing, Methodology, Data curation. **So Kawaguchi:** Writing – review & editing, Methodology, Data curation. **Michael C. Double:** Writing – review & editing, Methodology, Data curation. **Elanor M. Bell:** Writing – review & editing. **Ryosuke Makabe:** Writing – review & editing, Resources, Methodology, Formal analysis, Data curation. **Masato Moteki:** Writing – review & editing, Resources, Methodology, Formal analysis, Data curation. **Nils Hoem:** Writing – review & editing, Methodology, Data curation. **Brian Fry:** Writing – review & editing, Supervision, Methodology, Formal analysis. **Michele Burford:** Writing – review & editing, Supervision. **Susan Bengtson Nash:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.172939.

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