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Southern Ocean humpback whale trophic ecology. I. Combining multiple stable isotope methods elucidates diet, trophic position and foraging areas

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ABSTRACT: Southern Ocean humpback whales *Megaptera novaeangliae* are capital breeders, breeding in the warm tropics/subtropics in the winter and migrating to nutrient-rich Antarctic feeding grounds in the summer. The classic feeding model is for the species to fast while migrating and breeding, surviving on blubber energy stores. Whilst northern hemisphere humpback whales are generalists, southern hemisphere counterparts are perceived as krill specialists, but for many populations, uncertainties remain regarding their diet and preferred feeding locations. This study used bulk and compound-specific stable isotope analyses and isoscape-based feeding location assignments to assess the diet, trophic ecology and likely feeding areas of humpback whales sampled in the Ross Sea region and around the Balleny Islands. Sampled whales had a mixed diet of plankton, krill and fish, similar to the diet of northern hemisphere humpback whales. Proportions of fish consumed varied but were often high (2–60%), thus challenging the widely held paradigm of Southern Ocean humpback whales being exclusive krill feeders. These whales had lower $\delta^{15}N$ values and trophic position estimates than their northern hemisphere counterparts, likely due to lower Southern Ocean baseline $\delta^{15}N$ surface water values and a lower percentage consumption of fish, respectively. Most whales fed in the Ross Sea shelf/slope and Balleny Islands high-productivity regions, but some isotopically distinct whales (mostly males) fed at higher trophic levels either around the Balleny Islands and frontal upwelling areas to the north, or en route to Antarctica in temperate waters off southern Australia and New Zealand. These results support other observations of humpback whales feeding during migration, highlighting the species' dietary plasticity, which may increase their foraging and breeding success and provide them with greater resilience to anthropogenically mediated ecological change. This study highlights the importance of combining *in situ* field data with regional-scale isoscapes to reliably assess trophic structure and animal feeding locations, and to better inform ecosystem conservation and management of marine protected areas.

KEY WORDS: Feeding ecology · $\delta^{15}N$ · $\delta^{13}C$ · Amino acids · MixSIAR · Isoscapes · Antarctica · UNSDG14 Life Below Water

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1. INTRODUCTION

Humpback whales *Megaptera novaeangliae* are balaenopterid cetaceans that are distributed throughout the world's oceans and are the most extensively studied of all large cetaceans (Fleming & Jackson 2011). Southern hemisphere humpback whales complete annual migrations of over 8000 km between cold, nutrient-rich Southern Ocean feeding grounds in summer, and warmer calving grounds (also often referred to as breeding grounds) in low-latitude waters in winter (Clapham 1996, 2018, Corkeron & Connor 1999). Along with gray whales *Eschrichtius robustus*, humpback whales have one of the longest recorded mammalian migrations (Clapham 2001, Rasmussen et al. 2007, Stevick et al. 2011). They are capital breeders, traditionally thought to fast during migration and breeding (Lockyer & Brown 1981), surviving on energy or 'capital' from their blubber stores built up from feeding on high-density prey patches during the feeding season (Hain et al. 1981, Hazen et al. 2009, Cade et al. 2020). However, uncertainties remain surrounding humpback whale movement patterns and mixing of different populations, their diet and their degree of feeding whilst migrating (Gales et al. 2009, Barendse et al. 2010, Owen et al. 2024, this volume). Given their large body size (12–17 m), high energy requirements and the importance of humpback whales as consumers in Southern Ocean food webs (Witteveen et al. 2006), there is a need to better understand their diet and foraging ecology to effectively manage and conserve this species and its associated ecosystems. This is particularly relevant considering the commercial harvesting of Antarctic krill *Euphausia superba* in the Scotia Sea region and ecosystem shifts resulting from global climate (Kawaguchi et al. 2013, Stock et al. 2014, Schine et al. 2016) and oceanic change (Nicol et al. 2008).

Humpback whales feed by lunge feeding, advancing on prey with their mouths open and engulfing large quantities of water, then closing their mouths, forcing water out through their baleen plates to trap filtered prey (Dolphin 1988, Baraff et al. 1991, Owen et al. 2017). In the northern hemisphere, they are classified as generalists, feeding on a mixed diet of fish and krill (Christensen et al. 1990, 1992, Ryan et al. 2014, Witteveen & Wynne 2016), whereas in the southern hemisphere, numerous studies have recorded humpback whales as feeding predominantly on krill (Matthews 1937, Chittleborough 1965, Kawamura 1994, Bannister & Hedley 2001, Paterson et al. 2001, Friedlaender et al. 2006, 2008, Waugh et al. 2012, Groß et al. 2020). Southern Ocean humpback whales were thought to confine their feeding to Antarctic waters, fasting whilst on their calving grounds and when migrating (Dawbin 1966, Lockyer 1981, Baraff et al. 1991). However, there is now increasing evidence of humpback whales feeding on high-density krill patches and fish during migration, both in the southern hemisphere (e.g. Gill et al. 1998, Stamation et al. 2007, Gales et al. 2009, Barendse et al. 2013, Eisenmann et al. 2017, Andrews-Goff et al. 2018, Owen et al. 2024) and northern hemisphere (Baraff et al. 1991, Swingle et al. 1993, Laerm et al. 1997, Visser et al. 2011). Indeed, 4 of the 7 humpback whale breeding populations have been observed to feed along migration routes (International Whaling Commission 2011), with feeding events lasting from days to weeks in highly productive temperate areas (Gales et al. 2009, Owen et al. 2015). Seasonal aerial surveys recorded regular aggregations of more than 20 humpback whales feeding on baitfish between 37 and 42° S off the coast of Australia during migration (D. Donnelly unpubl. data). Due to the mobile nature of these whales and the remote location of their foraging grounds, long-term tracking of individuals to establish feeding sites is logistically challenging and expensive. Standard techniques for tracking whale movements have included observations from whaling records and 'Discovery' tag data (Rayner 1939, Chittleborough 1959, Dawbin 1964), photo-identification (Garrigue et al. 2004, Constantine et al. 2014, Franklin et al. 2014), satellite tagging (Dalla Rosa et al. 2008, Riekkola et al. 2018) and genetic analysis (Constantine et al. 2014, Schmitt et al. 2014a,b, Steel et al. 2018). More recently, stable isotope analysis has emerged as a powerful tool to investigate the trophic ecology and foraging ranges of humpback whales by analysing the stable isotope values of their tissues and prey within their foraging environments (Eisenmann et al. 2016, Witteveen & Wynne 2016, MacKenzie et al. 2022).

The isotopic composition of phytoplankton at the base of the food chain (the isotopic baseline) is transferred to higher trophic levels with relatively predictable relationships (De Niro & Epstein 1978, 1981, Minagawa & Wada 1984, Vander Zanden & Rasmussen 1999). The bulk nitrogen stable isotope value (the ratio of ^{15}N to ^{14}N, expressed as $\delta^{15}N$ in ‰ units) in a consumer, such as a humpback whale, can be increased by 3–4 ‰ relative to its diet. This difference in isotopic composition, referred to variously as fractionation factor, tissue–diet (isotopic) spacing or trophic discrimination factor (TDF), makes nitrogen stable isotopes a valuable tool for trophic studies (Peterson & Fry 1987, Post 2002, Vander Zanden & Rasmussen 2001). However, TDFs can be variable within individuals, among species and within different environments (Vander Zanden & Rasmussen 2001,

McCutchan et al. 2003; see also Section 2.5.1 below), so knowledge of the species and ecosystem is important. Baseline $\delta^{15}N$ values can also vary greatly across space (Somes et al. 2010, McMahon et al. 2013, MacKenzie et al. 2014) and time (Schmittner & Somes 2016, Espinasse et al. 2019, St John Glew & Espinasse et al. 2021), so the importance of mapping phytoplankton $\delta^{15}N$ values to estimate the trophic position (TP) of consumers in food webs is widely recognised (Hobson & Welch 1992, Cabana & Rasmussen 1996, Jennings & Warr 2003). Complementary to baseline and consumer tissue bulk $\delta^{15}N$ analysis, an additional assessment of TP can be made via compound-specific stable isotope analysis (CSIA) of nitrogen in amino acids (N-AA), using $\delta^{15}N$ values of certain amino acids ($\delta^{15}N_{AA}$) (McClelland & Montoya 2002, Chikaraishi et al. 2009, 2014). This approach is based on the fractionation between the so-called 'source' and 'trophic' amino acids in metabolic processes (Popp et al. 2007, Hannides et al. 2009). Source amino acids cannot be synthesised and must be acquired through diet; therefore, their $\delta^{15}N$ values reflect the isotopic baseline, whereas trophic amino acids can be acquired or synthesised, and their $\delta^{15}N$ values reflect the isotopic baseline plus trophic and physiological effects. As ^{14}N is preferentially excreted, exchange of nitrogen with the available nitrogen pool results in an enrichment in ^{15}N in an organism's tissue as biomass is transferred from one trophic level to another, thereby increasing $\delta^{15}N_{AA}$ values of trophic amino acids in secondary consumers (Hannides et al. 2009, Chikaraishi et al. 2014). Thus, a general equation based on $\delta^{15}N_{Glx}$ (glutamic acid, trophic) and $\delta^{15}N_{Phe}$ (phenylalanine, source) can be used to assess the TP ($TP_{Glx/Phe}$) of any organism across different environments (Chikaraishi et al. 2009, 2014; see also Section 2.6).

Carbon is less affected by trophic fractionation than nitrogen, with an approximate 0.4–0.8 ‰ increase per trophic level (Vander Zanden & Rasmussen 2001, Post 2002). This means that bulk carbon stable isotope values (the ratio of ^{13}C to ^{12}C, expressed as $\delta^{13}C$ in ‰ units) are more suitable to trace the source of carbon to an organism or system, where sources are isotopically distinct (Fry & Sherr 1984, Rounick & Winterbourn 1986, France & Peters 1997). Nevertheless, carbon stable isotopes also show variable trophic enrichment and highly dynamic baseline values. Pelagic suspended particulate organic matter (SPOM), a proxy for marine phytoplankton (which strictly speaking comprises phytoplankton and detritus) in open-ocean waters, shows a positive relationship between water temperature and $\delta^{13}C$ values (Sackett et al. 1965, Rau et al. 1989, Goericke & Fry 1994). The relationship is particularly strong in the Southern Ocean between 40 and 80° S, where persistent $\delta^{13}C$ gradients have been measured (Cherel & Hobson 2007, Quillfeldt et al. 2010, Espinasse et al. 2019). The predictable relationship between $\delta^{13}C$ values of SPOM and spatially determined environmental variables has enabled the development of both data- and process-based models of natural spatio-temporal variations in isotopic baselines, which are termed isoscapes. These models enable trophic levels and diet (St John Glew et al. 2018), feeding grounds (Cherel & Hobson 2007, Cherel et al. 2007, Jaeger et al. 2010) and movements or migrations of marine organisms (Graham et al. 2010, Hobson et al. 2010, Trueman et al. 2019) to be inferred from consumer tissue isotope data. Isoscape applications are now widespread and summarised in several review papers (Hobson 1999, Ramos & González-Solís 2012, Trueman et al. 2012, McMahon et al. 2013, Trueman & St John Glew 2019), and the recent development of large-scale oceanic modelled isoscapes for carbon (Magozzi et al. 2017, St John Glew & Espinasse et al. 2021) and nitrogen stable isotopes (Somes et al. 2010, Schmittner & Somes 2016, St John Glew & Espinasse et al. 2021) has increased confidence in large basin-scale animal movement inferences from tissue stable isotope values.

This study focussed on humpback whales feeding during the summer months in the vicinity of the Balleny Islands and the Ross Sea slope, East Antarctica, a known high-density feeding ground (Franklin et al. 2012, Harrison et al. 2020). Animals feeding in this region most likely belong to groups of humpback whales that migrate in the autumn to calving grounds in north-eastern Australian and New Caledonian waters (Constantine et al. 2014, Schmitt et al. 2014a, Riekkola et al. 2018), classified by the International Whaling Commission (2011) as the E1 breeding population. The hypothesis that 'Southern Ocean humpback whales have a similar diet to northern hemisphere humpback whales, eating a mixed diet of fish and krill' was tested. Combining multiple stable isotope methods and data from three voyages to the Balleny Islands and Ross Sea, the TP, diet and likely feeding locations of humpback whales were determined. After examining the whale isotopic niche data, the hypothesis that 'some whales may feed at higher trophic levels than others' was also explored through modelling the relative proportions of prey taken by whales occupying different isotopic niches and through CSIA analysis. A literature review of carbon and nitrogen stable isotope and TP values was completed to compare Southern Ocean humpback whales of this study with northern hemisphere populations.

2. MATERIALS AND METHODS

2.1. Overview

Surface water SPOM (used as a proxy for phytoplankton in this study) was sampled along transect lines from New Zealand to the Ross Sea to provide baseline data for estimates of whale TP and to generate field data to validate $\delta^{13}C$ and $\delta^{15}N$ isoscapes. A combination of $\delta^{13}C$ and $\delta^{15}N$ analyses of whale skin biopsies and muscle from potential whale prey, and CSIA of N-AA of the whale skin were used to determine the diet and TP of humpback whales sampled around the Balleny Islands and the Ross Sea slope. The TP of the whales was validated using a Bayesian estimate of TP (Quezada-Romegialli et al. 2018). Bayesian modelling was used to determine niche width and isotopic niche overlap to assess if whale clusters were isotopically distinct (Jackson et al. 2011). In addition, 'MixSIAR' (Bayesian Mixing Models in R) modelling (Stock et al. 2018) was applied to determine the proportions of prey that humpback whales were feeding on. Finally, data-derived and modelled $\delta^{13}C$ and $\delta^{15}N$ isoscapes (St John Glew & Espinasse et al. 2021) were used to ascertain where the humpback whales were most likely to have been feeding over the integrated time period of their skin biopsy record.

2.2. Study area and sampling

2.2.1. Study area

Biological samples were collected during 3 oceanographic voyages from New Zealand to the Ross Sea on the RV *Tangaroa*: (1) International Polar Year — Census of Antarctic Marine Life voyage, January–March 2008 (Pinkerton et al. 2011); (2) Antarctic Whale Expedition voyage, February–March 2010 (Gales 2010 https://data.aad.gov.au/aadc/voyages/display_voyage.cfm?voyage_id=544); and (3) New Zealand–Australia Antarctic Ecosystems voyage, February–March 2015 (O'Driscoll & Double 2015). Henceforth the sampling trips are referred to respectively as (1) V2008, (2) V2010 and (3) V2015, where 'V' represents 'voyage'. The vessel tracks for each voyage and the key sampling locations of SPOM and marine fauna are shown in Figs. 1 & 2. Whale skin and SPOM samples were collected during V2010 and V2015, and prey samples were collected on all 3 voyages. Details of the sample types and numbers taken on each voyage are provided in Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m734p123_supp1.pdf.

2.2.2. SPOM sampling and processing

SPOM samples were obtained by underway sampling of near-surface water at 6-hourly intervals from 5.5 m beneath the RV *Tangaroa* via the Underway Flow Through System on V2010 and V2015 (Fig. 1). For sample processing details, see Text S1.

2.2.3. Humpback whale biopsy sampling and tissue processing

A total of 65 humpback whale biopsies were sampled for stable isotope analysis, genetics and sex determination (Table S1, Text S2), with 55 biopsies obtained between 12 February and 8 March 2010, and 10 biopsies sampled between 7 February and 2 March 2015 (Fig. 1). The arrival time of humpback whales on their Antarctic feeding grounds is between October and December (Chittleborough 1965, Dawbin 1966, Andrews-Goff et al. 2018). Given an estimated skin turnover rate of 3 to 4 mo (Text S3), for skin biopsies taken in February/March, the stable isotopic composition of a whale's prey should be almost fully integrated into the whale skin after 3 to 5 mo of feeding. The measured isotopic values of the whale skin were therefore expected to primarily reflect the Antarctic feeding ground signal.

In 2010, 31 biopsies were sampled in the vicinity of the Balleny Islands (BI: 162.0–166.0° E, 66.0–67.5° S), 22 south-east of the Balleny Islands (SEBI: 166.0–170.0° E, 67.5–70.0° S) and 2 along the Ross Sea slope (RSS: 175.0° E–165.0° W, 69.0–70.5° S). In 2015, 7 humpback whales were sampled around BI and 3 along the RSS. For detailed sampling methods and processing information, see Text S2.

2.2.4. Prey sampling and analytical preparation

Sampling locations of fish, Antarctic krill and mixed community zooplankton (which were not identified to species) are shown in Fig. 2, with sample numbers provided in Table S1 and methods and tissue processing details in Text S4. The fish sampled included 5 myctophid (lantern fish) species (*Electrona carlsbergi*, *E. antarctica*, *Gymnoscopelus nicholsi*, *G. opisthopterus* and *G. braueri*) and Antarctic silverfish *Pleuragramma antarctica*. These species were the only prey species sampled that were deemed to be relevant as potential humpback whale prey and together are amongst the most commonly encountered fish in the Southern Ocean (Koubbi et al. 2011, Woods et al. 2023).

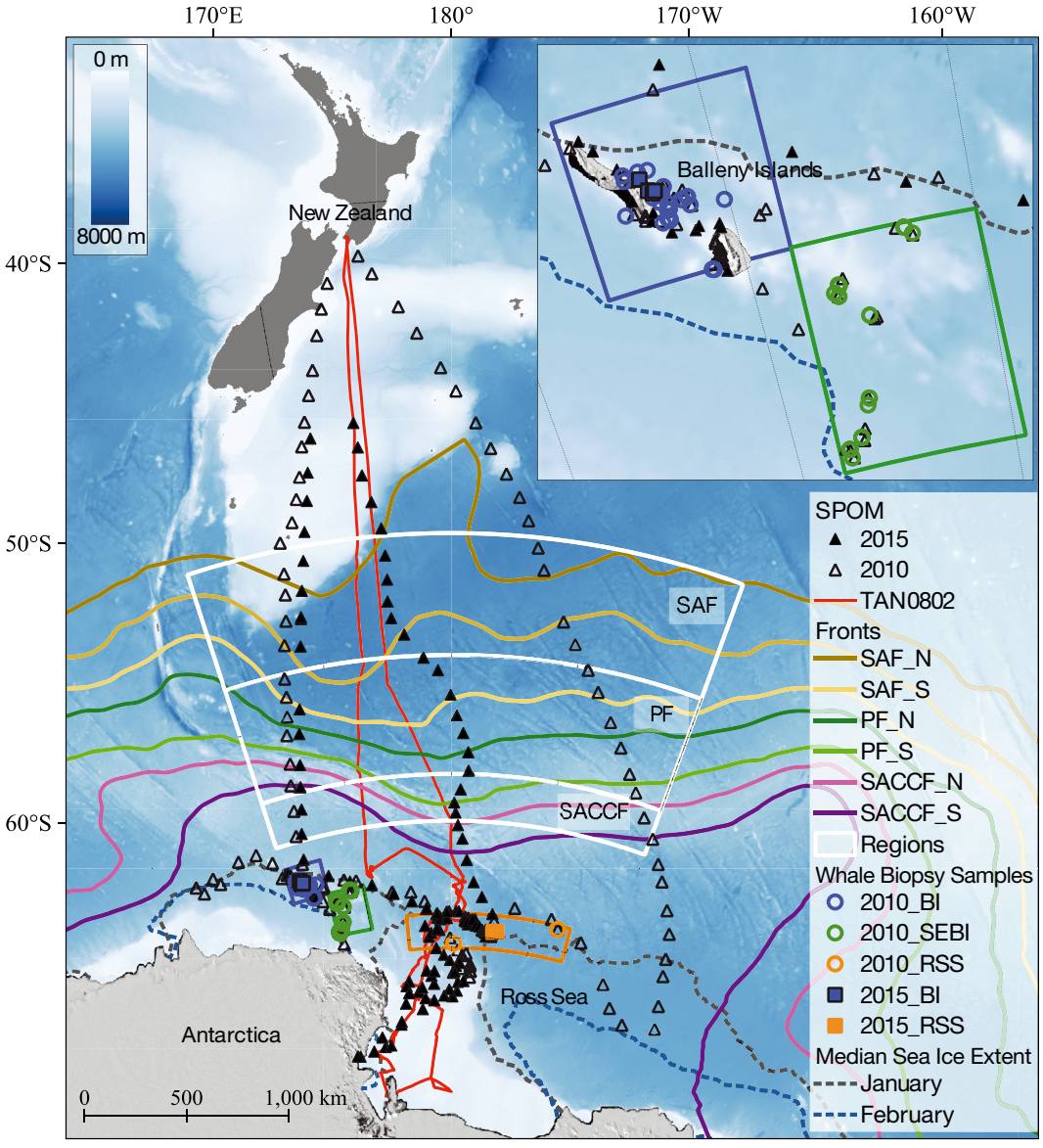

Fig. 1. Location of ship's voyage (V) tracks, suspended particulate organic material (SPOM) and humpback whale *Megaptera novaeangliae* biopsy sampling during V2008, V2010 and V2015. SPOM sampling locations indicate the ship's tracks in 2010 and 2015; the ship's track in 2008 is marked by the solid red line (no SPOM samples were taken on this voyage). The inset shows finer-scale details of humpback whale skin sampling locations around the Balleny Islands (BI). SEBI: south-east Balleny Islands; RSS: Ross Sea slope. The locations of the major oceanographic fronts (after Sokolov & Rintoul 2007) are marked as SAF_N (Subantarctic Front, northern boundary), SAF_S (Subantarctic Front, southern boundary), PF_N (Polar Front, northern boundary), PF_S (Polar Front, southern boundary), SACCF_N (Southern Antarctic Circumpolar Current Front, northern boundary) and SACCF_S (Southern Antarctic Circumpolar Current Front, southern boundary). The location of the median sea ice extent between 1981 and 2010 is also included for the months of January and February using data from the National Snow and Ice Data Center (Fetterer et al. 2017). Bathymetry was generated from the General Bathymetric Chart of the Oceans (GEBCO), sourced online at https://www.gebco.net/data_and_products/gridded_bathymetry_data/

2.2.5. Lipid extraction of biological samples

Lipid synthesis strongly discriminates against the ^{13}C isotope (De Niro & Epstein 1977, 1978), leading to more negative $\delta^{13}C$ values in lipid-rich tissues, relative to proteins and carbohydrates (Rounick & Winterbourn 1986). To reduce bias in stable isotope results due to 'lipid contamination' (Hebert & Keenleyside 1995, Post et al. 2007, Mintenbeck et al. 2008), we followed the recommended method of analysing bulk (whole) samples for nitrogen content (%N) and $\delta^{15}N$ values, and lipid-extracting samples to obtain accurate carbon content (%C) and $\delta^{13}C$ values (Ricca et al. 2007, Logan et al. 2008) for all whale biopsy

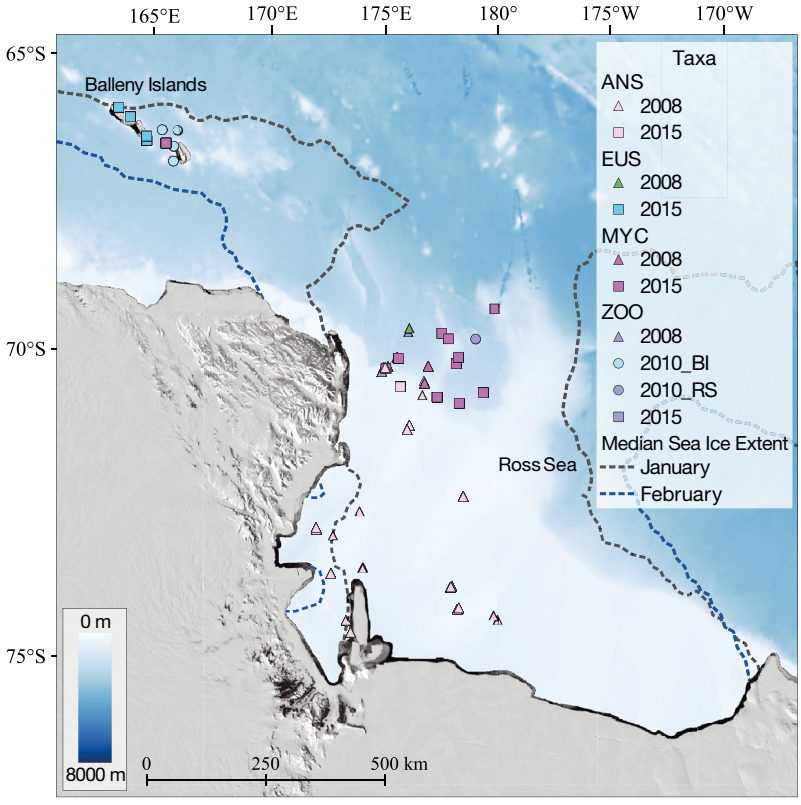

Fig. 2. Sampling locations of potential humpback whale *Megaptera novaeangliae* prey samples taken during voyages (V) V2008, V2010 and V2015. ZOO: zooplankton; EUS: Antarctic krill *Euphausia superba*; MYC: myctophids (5 species: *Electrona carlsbergi*, *E. antarctica, Gymnoscopelus nicholsi*, *G. opisthopterus* and *G. braueri*); ANS: Antarctic silverfish *Pleuragramma antarctica*; BI: Balleny Islands; RS: Ross Sea. The colours of the species symbols match those in Fig. 5

(V2010, V2015), krill (V2008) and myctophid (V2010, V2015) samples (methodological details in Text S5). Krill (V2015) and silverfish (V2008, V2015) were analysed as whole bulk samples, with a subset analysed after lipid extraction to derive a species-specific $\delta^{13}C$ correction formula. Where bulk C:N mass ratios exceeded 3.5, we corrected the $\delta^{13}C$ values using these derived formulae. For mixed-community zooplankton samples, where sample material was limited, $\delta^{13}C$ data were corrected for lipid content using C:N molar ratios following equations in Fry (2002).

2.3. Stable isotope analysis

2.3.1. Bulk stable isotope analysis

All bulk stable isotope analyses were carried out at the NIWA Environmental and Ecological Stable Isotope Analytical Facility in Wellington, New Zealand, using 2 intercalibrated elemental analyser (EA) continuous flow isotope ratio mass spectrometer (CF-IRMS) analytical systems. Most analyses were carried out using a MAS200 autosampler connected to a Flash 2000 EA coupled with a DELTA V Plus (Thermo Fisher Scientific) CF-IRMS. A small number of samples were analysed using an AS200_LS autosampler on an NA-1500 EA (Fisons Instruments) linked to a DELTA^{Plus} CF-IRMS (Thermo Fisher Scientific). For details of analysis, standards used, isotopic calculations and normalisation, accuracy and precision, refer to Text S6. All estimates of variance reported are given as ±1 SD, using the format 'mean, SD'.

2.3.2. Amino acid hydrolysis and derivatisation for CSIA of whale biopsy samples

Fourteen humpback whale skin samples were selected for CSIA of $\delta^{15}N_{AA}$ from Clusters A and B (see Section 2.4.2), from samples where sufficient skin biopsy material was available to encompass the maximum range of bulk isotope values and both sexes (8 males and 6 females). One sample was analysed in duplicate providing replication of analysis (Table S2: sample 2010_216a and b). Amino acids are non-volatile molecules that require hydrolysis and derivatisation prior to analysis. Whale biopsy samples were hydrolysed into individual amino acids with 6 N hydrochloric acid, then derivatised using acetyl chloride-isopropanol followed by trifluoroacetic anhydride to produce trifluoroacetic amino acid esters (Macko et al. 1997). The hydrolysis and derivatisation method of Hannides et al. (2009) was closely followed with only minor deviations, which are reported in Text S7.

2.3.3. CSIA of N-AA

Derivatised samples were transferred into ethyl acetate and diluted to the appropriate concentration for analysis on the gas chromatograph (GC) IRMS. Eleven amino acids were detected and reported: 7 'trophic' amino acids (alanine, valine, leucine, isoleucine, proline, aspartic acid and glutamic acid), a 'source' amino acid (phenylalanine), a 'metabolic'

amino acid (threonine) and 2 'intermediate' amino acids (glycine and serine). Glycine and serine cannot easily be classified as either 'source' or 'trophic' amino acids (Cherel et al. 2019) and are thus considered 'intermediate' (Shen et al. 2021).

The CSIA of N-AA was carried out on a TRACE Ultra GC with GC IsoLink interface coupled via a ConFlo IV to a DELTA V Plus IRMS (Thermo Fisher Scientific), with GC PAL autosampler (CTC Analytics). For details of the analysis, standards used, raw data corrections, accuracy and precision refer to Text S8 and Fig. S1.

2.4. Statistical analyses

2.4.1. Comparing stable isotope values between locations, age groups and sexes

Differences in $\delta^{13}C$ and $\delta^{15}N$ values between locations (BI, SEBI, RSS), age groups (adult, subadult, dependent young) and sexes of whales were investigated using generalised linear models (GLMs) with a Gaussian distribution and an identity link function. Twelve models were built for $\delta^{15}N$ and $\delta^{13}C$, respectively, including all possible combinations of variables. Models were then ranked according to their Akaike's information criterion (AIC) corrected for small sample sizes (AIC_C) (Burnham et al. 2011) to select the model that best explained the data. Final models were checked for interactions between variables and homogeneity of variance, and residual distributions were checked for normality. All statistical analyses were completed in R (R Core Team 2020).

2.4.2. Niche comparison

K-means cluster analysis (MacQueen 1967, Lloyd 1982) was used to define 2 clusters (A and B) of humpback whales based on their respective $\delta^{13}C$ and $\delta^{15}N$ values. K-means clustering is an established unsupervised machine learning algorithm for segregating a data set into *k* groups or clusters, where *k* represents the number of clusters pre-specified by the user (here, $k = 2$, chosen *a priori* after visual inspection of the data), and objects within the same cluster are as similar as possible.

Six different Layman metrics ($\delta^{13}C$ range, $\delta^{15}N$ range, total area [TA], mean distance to centroid [CD], mean nearest neighbour distance [MNND] and standard deviation of nearest neighbour distance [SDNND]) (Layman et al. 2007) were used to compare isotopic niches between clusters (Table S3). All Layman metrics were bootstrapped with replacement (n = 10 000, indicated with a subscript '$_{boot}$') based on the smallest sample size in the data set (n = 9) to enable statistical comparison between clusters (Manly 1997, Jackson et al. 2012). To further assess niche widths and isotopic niche overlap between clusters, standard ellipse areas (SEAs), the bivariate equivalent to standard deviation in univariate analyses, were calculated with correction for small sample size (SEAc, Jackson et al. 2011). In addition, Bayesian SEAs (SEA_B) were calculated using 1000 posterior draws to statistically compare niche width and to estimate the niche overlap between clusters, calculated as the proportion of the total SEA_B for each sex, respectively. All metrics were calculated using the R package 'SIBER' (Stable Isotope Bayesian Ellipses in R) (Jackson et al. 2011, R Core Team 2020).

2.5. Prey apportionment modelling

2.5.1. Selection of diet–tissue TDFs

Quantifying the diet of an organism using prey apportionment modelling requires knowledge of the isotopic enrichment (i.e. TDF) in the predator relative to prey (DeNiro & Epstein 1978, 1981). TDFs can be highly variable depending on species, physiology, ontogeny, habitat and food type (see summary by Boecklen et al. 2011, their Table 1), and in large marine mammals, they are difficult to measure. However, from a study of wild fin whales *Balaenoptera physalus* feeding exclusively on euphausiid krill *Meganyctiphanes norvegica*, Borrell et al. (2012) calculated whale skin stable isotope TDFs of 1.28, 0.38 ‰ for carbon and 2.82, 0.30 ‰ for nitrogen. The authors suggested that TDFs are relatively constant between taxonomically close species and that fin whale values can be extrapolated to other cetaceans. Therefore, the TDF values of Borrell et al. (2012) (hereafter referred to as 'Borrell TDF') were used, but for comparison, data are also presented in the Supplementary Materials using the traditionally accepted Post (2002) stable isotope TDF values of 0.39, 1.3 ‰ for carbon and 3.4, 0.98 ‰ for nitrogen (hereafter referred to as 'Post TDF').

2.5.2. Mixing model

The contribution of different prey sources to the humpback whale diet was estimated using 2 isotopic tracers ($\delta^{13}C$ and $\delta^{15}N$), applying the isotopic mixing model of Stock et al. (2018), which incorporates

uncertainties in isotope values of both sources and consumers, TDFs and tissue turnover rates. The model included $\delta^{13}C$ and $\delta^{15}N$ values from 5 potential prey (phytoplankton, mixed community zooplankton, Antarctic krill, myctophids and silverfish), from 3 sampling locations (BI, RSS and Ross Sea [RS]). Phytoplankton were included as possible prey, as potentially significant proportions of phytoplankton can be entrained and consumed during the feeding filtration process, particularly in densely aggregated patches of food. These various combinations of prey stable isotope values and locations were grouped using Ward's hierarchical cluster analysis based on the mean $\delta^{13}C$ and $\delta^{15}N$ values of the prey (Fig. S2) to minimise the number of sources within the mixing model (Phillips & Gregg 2003, Moore & Semmens 2008, Parnell et al. 2010). Data were checked for normal distribution using a Shapiro-Wilk *t*-test and visual inspection (Table S4). To test the hypothesis that some of the male humpback whales may have been feeding at higher trophic levels than the rest of the sampled males and most females (see Section 3.2), data were modelled to work out the relative proportions of prey taken by whales in the 2 clusters (A and B; see Section 2.4.2).

To test whether data met the point-in-polygon requirement for every consumer (i.e. that all consumer isotopic values lie within a polygon bounded by the isotopic signatures of the sources; Phillips & Gregg 2003, their Fig. 6A–F), a simulated mixing polygon was computed (Smith et al. 2013). No tissue correction factor was applied to whale skin stable isotope data when plotted with whale prey muscle stable isotope data, as previous analysis of necropsied Hector's dolphin *Cephalorhynchus hectori*, Māui dolphin *C. h. maui* and killer whale *Orcinus orca* skin and muscle samples showed minimal fractionation for carbon or nitrogen stable isotopes between these 2 tissue types (S. Bury unpubl. data). Similar findings were reported for fin whales by Borrell et al. (2012) and for humpback whales by Todd et al. (1997), who reported differences of less than 0.4 ‰ between whale skin and muscle.

Two iterations of 'MixSIAR' were run using, firstly, the Post TDF (reported only in the Supplement) and, secondly, the Borrell TDF (reported in Section 3). To test which factors were involved in predicting dietary proportions, for each TDF, the null model including all whales with no clustering was compared with the model including the variable 'whale cluster' as a fixed categorical effect with 2 levels (Cluster A and Cluster B) (Table S5). Models had a multiplicative error term (Stock & Semmens 2016) and specifications were 3 Markov chain Monte Carlo (MCMC) chains, 200 000 iterations as burn-in, and 100 000 iterations thinned by a factor of 100, providing a total of 3000 draws for estimating posterior distributions and credible intervals. Model diagnostics were checked to ensure convergence, and models were evaluated by comparing their AIC weights (*w*AIC) (Burnham & Anderson 2002) and approximate leave-one-out cross-validation information criterion (LOO_{ic}) (Vehtari et al. 2017).

2.6. Estimation of humpback whale TP

Due to the difficulty of directly measuring a TDF for humpback whales, 3 different methods of TP calculations were applied to corroborate the results:

(1) simple mathematical TP estimates using SPOM, whale prey and whale $\delta^{15}N$ data from this study, combined with best estimates of TDFs between the consumer and the prey, taken from the literature (details provided in Section 3);

(2) a Bayesian estimation of TP from consumer stable isotope ratios using the R package 'tRophicPosition' (Quezada-Romegialli et al. 2018), which enables within-population variability to be accounted for and considers uncertainties and error propagation of the calculations. For the Bayesian model, krill were used as the nitrogen stable isotope baseline. Carbon stable isotope data were not incorporated in the model, as $\delta^{13}C$ values in this study were primarily driven by latitudinal feeding location, which would confound the TP estimates.

(3) TP estimates from CSIA data. Using the CSIA data, Eq. (1) (based on $\delta^{15}N$ values for the 'trophic' amino acid glutamic acid [$\delta^{15}N_{Glx}$] and the 'source' amino acid phenylalanine [$\delta^{15}N_{Phe}$]), was used to assess the TP ($TP_{Glx/Phe}$) of the humpback whales (Chikaraishi et al. 2009, 2014):

$$TP_{Glx/Phe} = [\delta^{15}N_{Glx} - \delta^{15}N_{Phe} - \beta / TDF] + 1 \quad (1)$$

where β represents the isotopic difference between $\delta^{15}N_{Glx}$ and $\delta^{15}N_{Phe}$ in primary producers (taken to be +3.4, 0.9 ‰ for marine algae). In a recent review, Ramirez et al. (2021) showed that β-values are taxon- and tissue-specific, but they also noted that variability in β-values dissipates at higher trophic levels. Therefore, the widely accepted marine algal value of +3.4 ‰ was used. The validity of the $TP_{Glx/Phe}$ estimate depends on the consistency of both β and TDF values (Chikaraishi et al. 2014, Ramirez et al. 2021). In this study, the humpback whale data-derived TDF value used for the $TP_{Glx/Phe}$ calculations was based on a whale TP of 3.32 (taken from the simple mathematical TP estimate (1) above; see also Section 3.6.1), where:

$$TDF_{whale} = (Glx - Phe - 3.4)/(TP_{whale} - 1), \text{ where } TP_{whale} = 3.58 \quad (2)$$

2.7. Isoscapes

Whale skin $\delta^{13}C$ values for individuals from Clusters A and B (as defined by the K-means cluster analysis) were used to identify the spatially explicit posterior probability for the origin of food resources incorporated into skin tissue of each individual whale. Assignment methods followed Wunder (2010) and were implemented with the R package 'ASSIGNR' (Ma et al. 2020) using carbon and nitrogen isoscape models for SPOM in the Southern Ocean (St John Glew & Espinasse et al. 2021). Since whale tissue of known origin was not available, $\delta^{13}C$ and $\delta^{15}N$ whale tissue values were adjusted by assuming a constant offset between whale skin and the isoscape model for SPOM of 1.67 ‰ for carbon (0.39 ‰ phytoplankton–krill Post TDF + 1.28 ‰ krill–whale Borrell TDF) and 6.22 ‰ for nitrogen (3.40 ‰ phytoplankton–krill Post TDF + 2.82 ‰ krill–whale Borrell TDF).

Spatially-explicit posterior probability densities were estimated for each whale individually. Assignments were first carried out using only $\delta^{13}C$ values and were then repeated using both $\delta^{13}C$ and $\delta^{15}N$ data. For the single $\delta^{13}C$-only isoscape assignments, the estimated variance model from St John Glew & Espinasse et al. (2021) was used. For the dual-isoscape assignments, single isotope variances estimated by St John Glew & Espinasse et al. (2021) were used for the diagonal of the variance–covariance matrix, and the off-diagonals were estimated from the expected values for $\delta^{13}C$ and $\delta^{15}N$ from the isoscape models for each raster cell (Ma et al. 2020). In both assignment model cases, the bounding box for the posterior densities ranged from 140 to 220° E and from 77.5 to 39.5° S. Probability densities were averaged across all whales in each of the 2 previously identified feeding Clusters A and B. The resultant probability densities are spatially explicit representations for the average feeding origin of the whales in each cluster.

2.8. Factors to consider when interpreting stable isotope data

Several factors should be considered when interpreting stable isotope data in the context of TP status, diet apportionment and feeding location assignments (Gannes et al. 1997, Jardine et al. 2006, Inger & Bearhop 2008). Useful summaries are provided by Bearhop et al. (2004) and in review papers by Martínez del Rio et al. (2009), Newsome et al. (2010), Boecklen et al. (2011) and Thomas & Crowther (2015). Briefly, factors include stable isotope incorporation rates into an animal's tissue and the metabolic activity of that tissue affecting its turnover rates (Text S3), tissue type correction factors (Cherel et al. 2005b), diet–tissue TDFs (Hobson & Clark 1992, Vander Zanden & Rasmussen 2001, Caut et al. 2009; Text S3), nutritional stress (Fuller et al. 2005), the sex, age, reproductive and physiological status of the organism (Fuller et al. 2004, Cherel et al. 2005a), estimates of stable isotope baselines (including the calculation of β-values in the CSIA TP calculation, Ramirez et al. 2021) and isoscape baseline-organism spacing values (see Section 2.7). Furthermore, isoscape-based animal assignments generally rely on isoscapes constructed using surface SPOM stable isotope values, which only provide an approximation of isotopic baselines, since SPOM stable isotope values vary with depth (Lourey et al. 2003), and both humpback whales and their prey undergo diel vertical movements. Varying degrees of uncertainty exist for all of these issues, with some information still unknown, generating caveats that need to be acknowledged.

3. RESULTS

3.1. Humpback whale skin stable isotope variability between sampling locations, whale age groups and sexes

Individual humpback whale skin $\delta^{13}C$ values ranged from −26.77 to −20.90 ‰, and $\delta^{15}N$ values ranged from 6.49 to 9.48 ‰ across all sampling locations and years with an overall arithmetic mean, ±1 SD (henceforth referred to simply as 'mean') of −25.23, 1.03 ‰ and 7.57, 0.66 ‰, respectively (Fig. 3; Table S1). A similar spread of $\delta^{13}C$ and $\delta^{15}N$ values occurred across all sampled regions (BI, SEBI and RSS), resulting in mean values overlapping between sampling regions and years. There was little isotopic variation in the mean and SD values of $\delta^{13}C$ and $\delta^{15}N$ values between adult whales sampled in 2015 (n = 10), and adults (n = 44), subadults (n = 6) and dependent young (n = 5) sampled in 2010 (Fig. S3b, Table S6).

Genetic analysis identified 29 males and 26 females sampled in 2010, with 1 male and 9 females sampled in 2015, giving a total of 30 male and 35 females sampled overall. The temporal sampling of males and females was evenly spread throughout the 2010 voyage. There

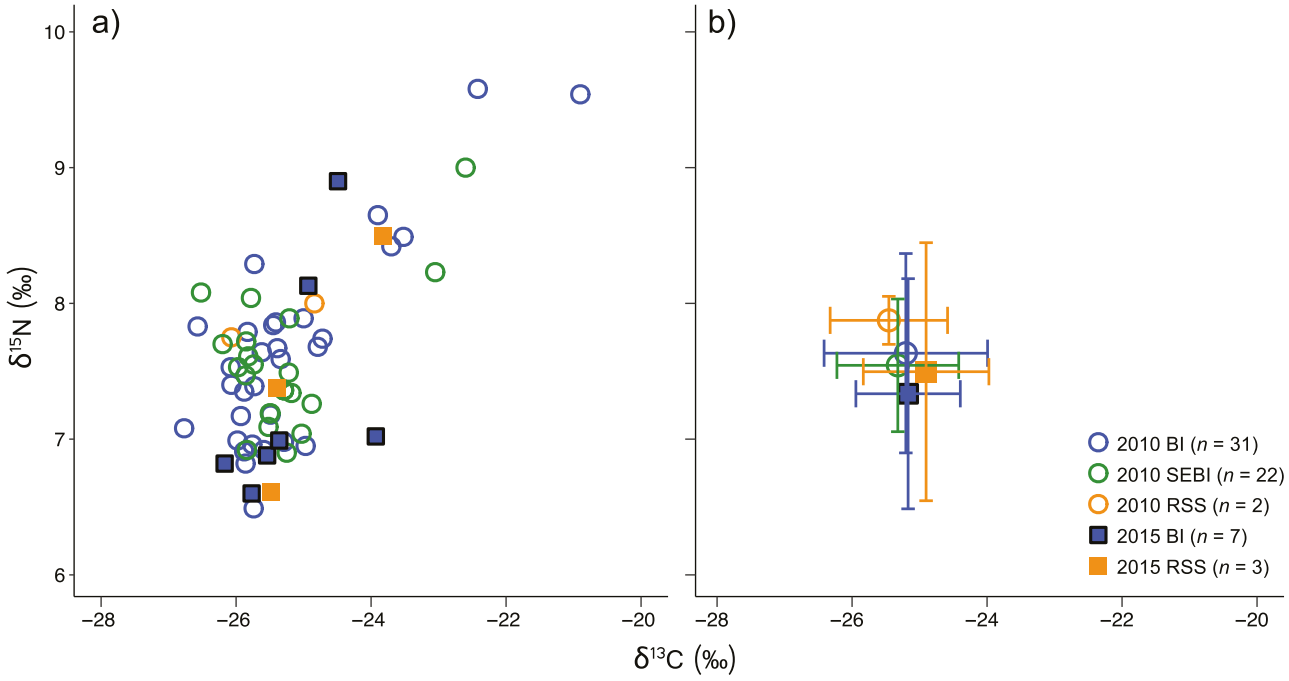

Fig. 3. Lipid-extracted $\delta^{13}C$ and bulk $\delta^{15}N$ biplot of 2010 and 2015 humpback whale *Megaptera novaeangliae* skin biopsy samples, showing sampling year and location for (a) all values and (b) mean ± 1 SD values. BI: Balleny Islands; SEBI: south-east Balleny Islands; RSS: Ross Sea slope; *n*: number of samples taken on each voyage in each region

was considerable overlap between male and female $\delta^{13}C$ and $\delta^{15}N$ values (Fig. S4), but across the data set, mean male values were slightly higher ($\delta^{13}C$: −24.86, 1.27 ‰; $\delta^{15}N$: 7.88, 0.65 ‰) than female values ($\delta^{13}C$: −25.56, 0.62 ‰; $\delta^{15}N$: 7.31, 0.55 ‰) (Table S7).

GLMs showed that sex, age and sampling year were the main predictors of both $\delta^{13}C$ and $\delta^{15}N$ values (Table S8). The top models retained sex and age for higher $\delta^{13}C$ values, and sex and year for higher $\delta^{15}N$ values. However, the second and third-best models for $\delta^{13}C$ (retaining sex and year; and sex, age and year) and the second-best models for $\delta^{15}N$ (retaining sex and year; and sex and age) explained the data almost equally well as the respective top-ranked models (Table S8). Values of $\delta^{15}N$ increased slightly with year, and dependent young had lower, and subadults had higher $\delta^{13}C$ values. However, although age and year were retained in the final models for $\delta^{13}C$ and $\delta^{15}N$ values, respectively, the effects were not significant (Table S9). While sex and age had comparable variable importance contributing to the overall model fit for $\delta^{13}C$ values, the final model for $\delta^{15}N$ values was mainly driven by sex (Fig. S5). The deviance explained was low for top-ranked models for both $\delta^{13}C$ and $\delta^{15}N$ values (18.9 and 17.9%, respectively), indicating that part of the data variation is not explained by the predictor variables.

3.2. Niche comparison

Two clusters (A and B) of individual humpback whales were identified, based on their respective $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 4). Cluster A whales had a mean $\delta^{13}C$ value of −25.57, 0.50 ‰ and a $\delta^{15}N$ value of 7.38, 0.43 ‰, whilst Cluster B whales had a mean $\delta^{13}C$ value of −23.66, 0.43 ‰ and $\delta^{15}N$ value of 8.81, 0.48 ‰ (Table S1); thus, Cluster B whales had 1.90 ‰ higher mean $\delta^{13}C$ and 1.43 ‰ higher mean $\delta^{15}N$ values than Cluster A whales. Isotopic niche metrics varied between the 2 clusters (Table S3), with Cluster B having a higher probability for larger bootstrapped values than Cluster A for all metrics, except MNND (97.2% Cluster A > Cluster B) and SDNND (79.2% Cluster A > Cluster B). Niche differentiation between the 2 clusters was further demonstrated by the negligible SEA_B overlap for both clusters (SEA_B overlap: Cluster A = 0.4%, Cluster B = 0.1%). Both clusters included whales sampled from all locations (BI, SEBI and RSS) (Fig. S6). However, Cluster B comprised predominantly male whales: 7 males and 2 females, with the 2 females plotting in the lower range of $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 4). This led to the hypothesis that some of the male humpback whales (those in Cluster B) may have been feeding at higher trophic

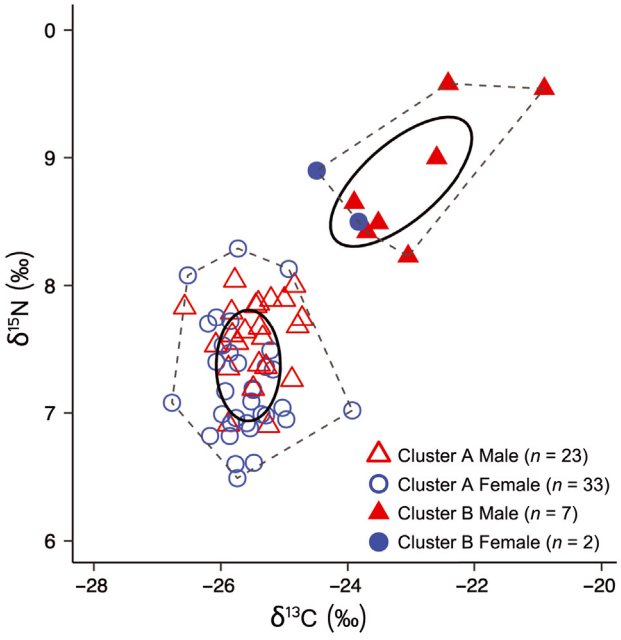

Fig. 4. Lipid-extracted $\delta^{13}C$ and bulk $\delta^{15}N$ biplot showing standard ellipse area corrected for small sample size (SEAc, solid line ovals) and convex hull area (TA, area within dotted lines) for humpback whales *Megaptera novaeangliae* (see Table S3 for definitions). Ellipse areas hold 40% of the data. See Fig. 3 to view year and location of whale biopsy samples and Fig. S3 to view whale age group, for each of the isotopically segregated clusters A and B

levels than the rest of the sampled males (those in Cluster A) and most females (Cluster A).

3.3. Carbon and nitrogen stable isotope values of humpback whale prey

Phytoplankton from all areas showed high variability in both $\delta^{13}C$ and $\delta^{15}N$ values, and this wide isotopic variability was reflected up the food chain and observed in mixed-community zooplankton, Antarctic krill, myctophids and Antarctic silverfish (Fig. 5a,b). BI phytoplankton had higher mean stable isotope values ($\delta^{13}C$: −24.05, 1.66 ‰; $\delta^{15}N$: 1.49, 0.95 ‰) than RSS ($\delta^{13}C$: −28.41, 1.01 ‰; $\delta^{15}N$: 0.39, 1.97 ‰) and RS phytoplankton ($\delta^{13}C$: −28.56, 0.98 ‰; $\delta^{15}N$: 0.06, 0.96 ‰), which were similar (Table S1). Antarctic krill from BI had higher isotope values ($\delta^{13}C$: −24.39, 1.07 ‰; $\delta^{15}N$: 4.96, 0.60 ‰) compared to Antarctic krill from RSS ($\delta^{13}C$: −26.23, 0.65 ‰; $\delta^{15}N$: 4.11, 0.62 ‰) and RS ($\delta^{13}C$: 26.09, 0.59 ‰; $\delta^{15}N$: 4.10, 0.62 ‰). The same pattern was also observed for BI mixed community zooplankton ($\delta^{13}C$: −23.39, 1.25 ‰), which had higher $\delta^{13}C$ values than mixed community zooplankton from the RSS ($\delta^{13}C$: −27.45, 1.01 ‰) and RS ($\delta^{13}C$: −27.19, 1.53 ‰). Notably, RSS mixed community zooplankton had higher $\delta^{15}N$ values (7.03, 2.04 ‰) compared to both RS ($\delta^{15}N$: 5.29, 2.26 ‰) and BI ($\delta^{15}N$: 4.81, 1.01 ‰) zooplankton. Myctophids from RSS and RS had similar $\delta^{13}C$ values (−25.5 ‰), with BI values 1 ‰ higher, and all 3 locations had similar $\delta^{15}N$ values, ranging from 9.08, 0.61 ‰ (RSS) to 9.57, 0.77 ‰ (RS). Myctophid $\delta^{13}C$ values overlapped with Antarctic silverfish values ($\delta^{13}C$: −25.11, 0.68 ‰), which had marginally higher $\delta^{15}N$ values (RS $\delta^{15}N$: 10.24, 0.8 ‰) than myctophids.

The isotopic prey polygon biplot (Fig. 5c) shows the isotopic means of the prey clusters (1−6, as defined based on the $\delta^{13}C$ and $\delta^{15}N$ values in Fig. S2), with the prey cluster numerals plotted in Fig. 5b,c. Humpback whale skin means (±1 SD) for 'all whales', 'Cluster A whales' and 'Cluster B whales' are shown with the Borrell TDF subtracted (Fig. 5c). The simulated mixing prey polygon plot (Smith et al. 2013) (Fig. S7) validated the use of these prey cluster data in the 'MixSIAR' prey apportionment mixing model (Stock et al. 2018) with the exemption of one outlier, which was removed from the data set used for the 'MixSIAR' model prior to analysis.

3.4. 'MixSIAR' mixing model outputs: proportions of different prey ingested by humpback whales

All prey clusters, i.e. 1−6 (Fig. S2), had significantly different means (*t*-tests) in one or both of the isotope ratios (Table S4). Myctophids and silverfish grouped together in Cluster 6 and are collectively referred to as 'fish' in the dietary discussion.

The Bayesian mixing model containing 'whale cluster' as a categorical variable was ranked highest (Table S5), and this model had lower multiplicative error terms (ξ_j) than the null model. The posterior distributions of the proportional contributions of each prey cluster to humpback whale diet for Borrell TDFs are shown in Fig. 6 and Table S10 (with results for Post TDFs provided for comparison in Fig. S8). Whilst the model outputs generate a range of possible prey proportions, the means of these ranges and the modes are also given in Figs. 6 & 8 and Table S10 to facilitate interpretation of the relative importance of each potential prey.

3.4.1. Cluster A whale diet

The dominant prey items for Cluster A whales were RSS and RS phytoplankton (Cluster 1: mean 34, 6%;

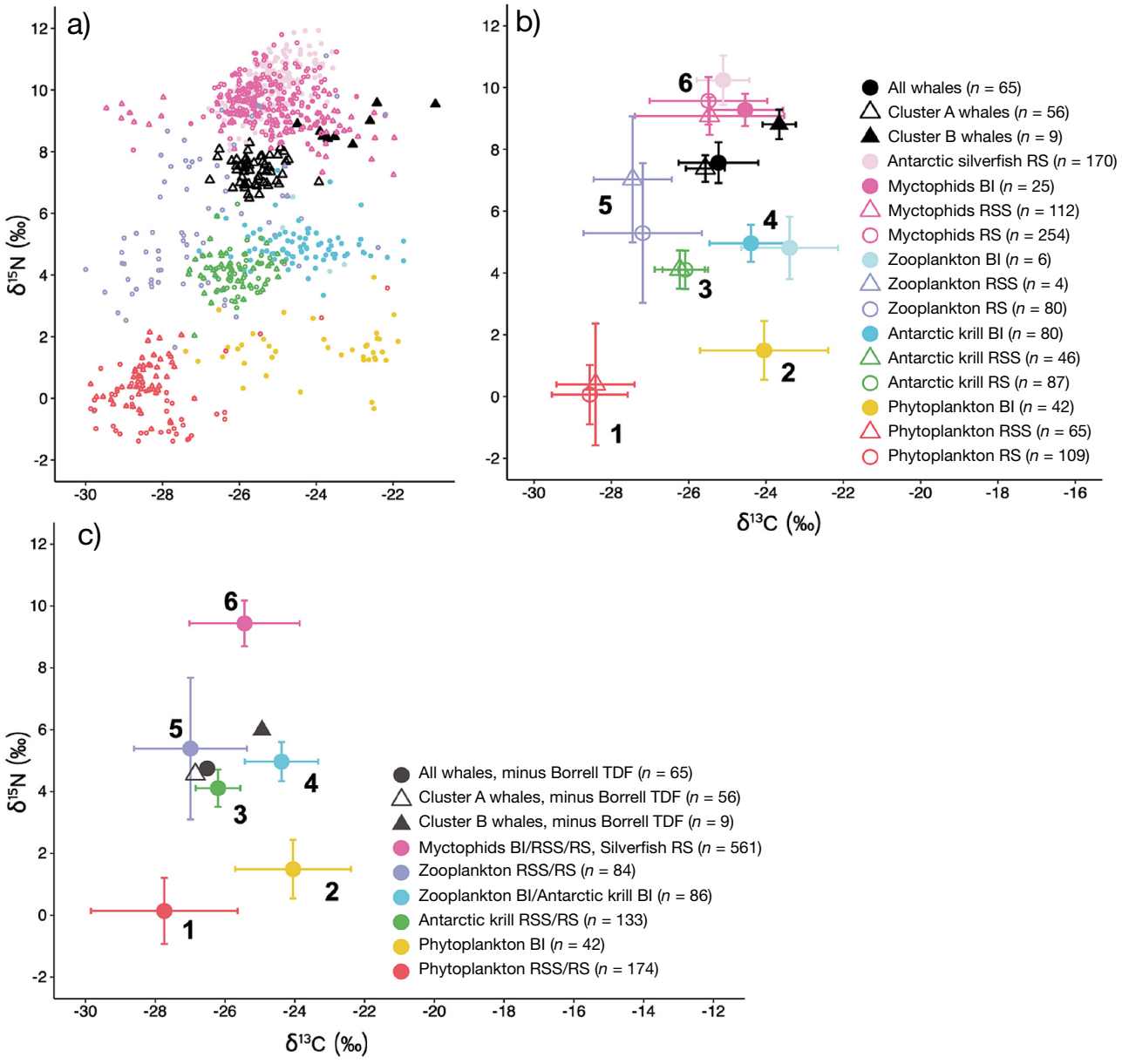

Fig. 5. (a) Lipid-extracted or lipid-corrected $\delta^{13}C$ and bulk $\delta^{15}N$ biplot of humpback whale *Megaptera novaeangliae* skin and muscle tissue of potential prey sampled in 2008, 2010 and 2015 from waters around the Balleny Islands (BI), the Ross Sea slope (RSS) and the Ross Sea (RS). (b) Mean values of data plotted in panel a. (c) Lipid-extracted or lipid-corrected $\delta^{13}C$ and bulk $\delta^{15}N$ prey polygon biplot showing means of potential humpback whale prey clusters. Humpback whale skin means are shown with the trophic discrimination factors (TDFs) of Borrell et al. (2012) subtracted. Error bars for whale skin isotope values are shown in panel b but have been omitted in panel c for image clarity. All means are plotted with ±1 SD. Symbol colours and **bold** black numbers represent the prey clustering used in Ward's hierarchical analysis (Fig. S2) and 'MixSIAR' Bayesian mixing model output results (Fig. 6)

range 11–50%), followed by fish (Cluster 6: mean 27, 7%; range 2–46%), and RSS and RS mixed-community zooplankton (Cluster 5: mean 25, 10%; range 1–57%) (Fig. 6a). Contributions from RSS and RS krill (Cluster 3), and BI phytoplankton (Cluster 2), mixed-community zooplankton and krill (Cluster 4) were minimal. Cluster A whales appeared therefore to be sourcing most of their diet from the RSS and RS.

3.4.2. Cluster B whale diet

Cluster B whales had a more varied diet than Cluster A whales, with the greatest proportion of their diet from BI mixed-community zooplankton and krill (Cluster 4: mean 41, 30%; range 0.1–83% with a bimodal result, meaning there were 2 plausible solutions for the proportion vector) (Fig. 6b). Fish (Cluster 6:

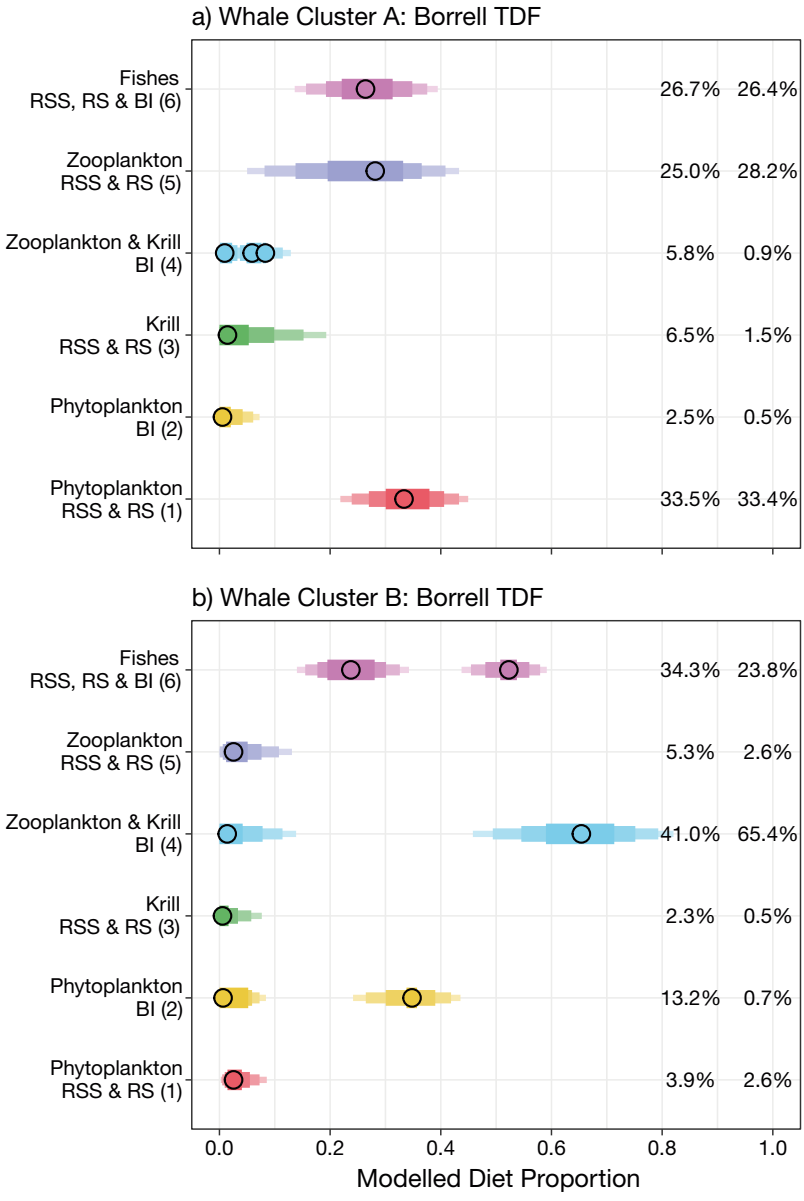

Fig. 6. Posterior distributions of the proportional contributions of each prey cluster (1–6, in parentheses) to the diet of humpback whales *Megaptera novaeangliae* estimated using 'MixSIAR' (Stock et al. 2018) applying the trophic discrimination factors (TDFs) of Borrell et al. (2012). Diets were estimated separately for whales in (a) Cluster A and (b) Cluster B. Posteriors are plotted as the highest probability density intervals (HPDIs), which represent the shortest interval width containing the desired credibility range, and are more appropriate when posteriors are skewed or multimodal compared to equal-tailed credible intervals. HPDIs of 50, 75, 90 and 95% are plotted for each prey cluster with decreasing bar thickness and colour intensity. Posterior peaks (modes) are plotted separately as filled circles. The posterior means and highest posterior peaks are given as percentages at the right-hand side of each panel for each prey cluster, with the mean given first on the left. RSS: Ross Sea slope; RS: Ross Sea; BI: Balleny Islands; Krill: Antarctic krill *Euphausia superba*; Fishes: mycotophids (*Electrona carlsbergi*, *E. antarctica, Gymnoscopelus nicholsi*, *G. opisthopterus* and *G. braueri*) plus Antarctic silverfish *Pleuragramma antarctica*. Numbers in brackets for the *y*-axis labels relate to Ward's hierarchical prey cluster numbers depicted in the dendrogram of Fig. S2

mean 34, 14%; range 3–60%, bimodal) and BI phytoplankton (Cluster 2: mean 13, 16; range 0–46%, bimodal) mostly made up the rest of their diet. Contributions from RSS phytoplankton, RSS and RS krill, and mixed-community zooplankton (Clusters 1, 3 and 5, respectively) were small. The bimodal results suggest that either (1) the diet was approximately two-thirds BI mixed-community zooplankton and krill with around a quarter fish and other minor components; or (2) that the diet was approximately 50% fish balanced by around one-third BI phytoplankton and little BI mixed-community zooplankton and krill. However, posterior modal peak heights suggest that the former diet is more probable. These results indicate a relative importance of fish in the diet of both Cluster A and B whales, and suggest that Cluster B whales derived a high proportion of their diet from around the BI.

3.5. CSIA of N-AA

Of the 14 humpback whale skin samples analysed for CSIA of N-AA, 9 were from Cluster A (5 males and 4 females) and 5 from Cluster B (3 males and 2 females) (Table S2). Values of $\delta^{15}N_{Glx}$ and $\delta^{15}N_{Phe}$, along with TP were plotted against bulk $\delta^{15}N$ data (Fig. 7). These plots illustrate a 'flat' trend line for $\delta^{15}N_{Phe}$, with those values remaining relatively constant with increasing bulk $\delta^{15}N$ values, compared to a steeper trendline for $\delta^{15}N_{Glu}$, which showed ^{15}N enrichment in glutamic acid as bulk $\delta^{15}N$ values increased. The AA $\delta^{15}N$ data were examined applying the amino acid 'fasting' and 'foraging' indicators outlined by Lübcker et al. (2020): mean $\delta^{15}N$ alanine values were similar between Cluster A (16.34, 5.43 ‰) and Cluster B whales (16.62, 3.50 ‰) (Table S2), whilst $\delta^{15}N$ threonine values were generally higher for Cluster B than Cluster A (mean −23.14, 3.01 ‰ compared to −27.82, 4.37 ‰, respectively), although high standard

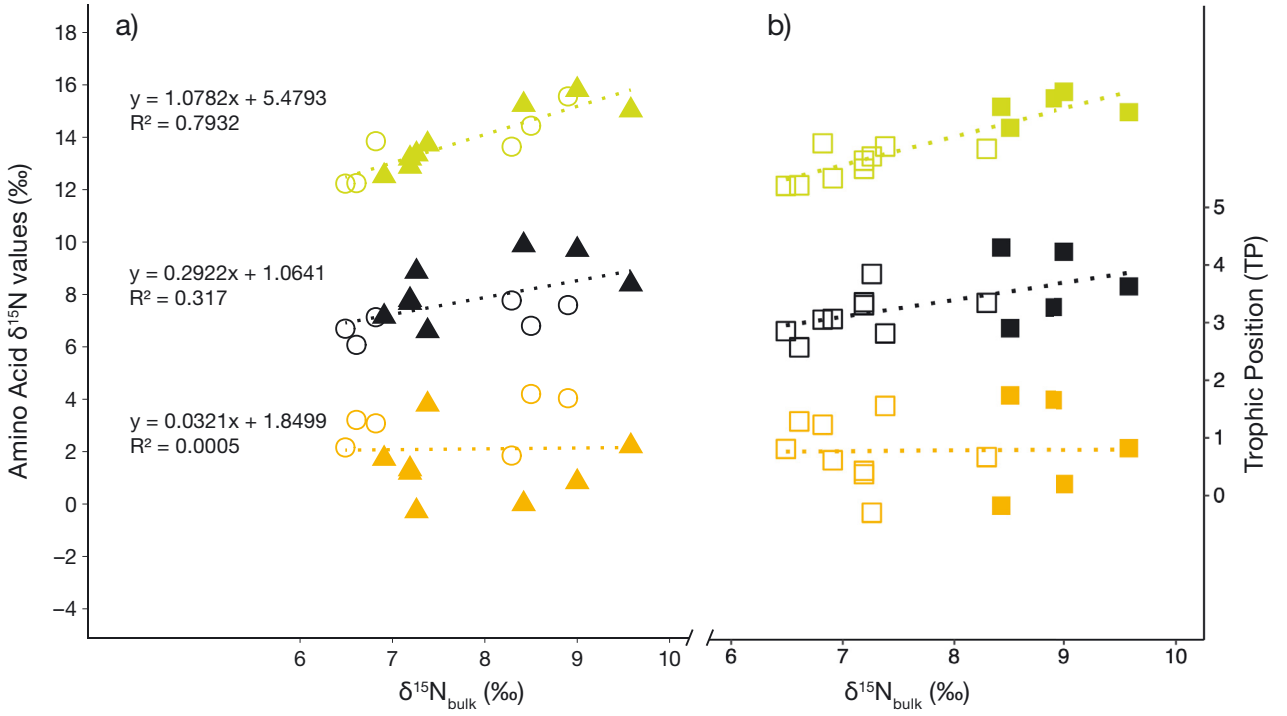

Fig. 7. Amino acid $\delta^{15}N$ values ($\delta^{15}N_{AA}$) of humpback whale *Megaptera novaeangliae* skin and whale trophic position (TP) plotted against bulk $\delta^{15}N$ values. Glutamic acid ('trophic amino acid') is shown in green, phenylalanine ('source amino acid') in orange and TP in black for (a) males (filled triangles) and females (open circles); and (b) whales in Cluster A (open squares) and Cluster B (filled squares)

deviations indicate there is considerable overlap in these data. No consistent trends were observed in any of the other amino acids.

3.6. Estimates of whale TP

Humpback whale $\delta^{15}N$ values ranged from 6.49 to 9.58 ‰ across the 65 skin biopsy analyses (Fig. 3; Table S1). This range of 3.1 ‰ corresponds to slightly more than 1 TP when applying the TDF of Borrell et al. (2012).

3.6.1. Simple mathematical TP calculation

A simple calculation of whale TP values (Table 1) was carried out using data presented in Table S11. Using bulk $\delta^{15}N$ data averaged over the years 2010 and 2015 for whales, and the years 2008, 2010 and 2015 for prey from all sampled regions south of 66° S, the following was noted. If the mean Southern Ocean phytoplankton baseline $\delta^{15}N$ value in regions where whales were most likely feeding is 0.45 ‰, the phytoplankton–krill TDF is 3.40 ‰ (Post 2002), and the krill–whale TDF is 2.82 ‰ (Borrell et al. 2012), then if whales were exclusively eating krill, one would expect their mean $\delta^{15}N$ isotope value to be 0.45 + 3.40 + 2.82 = 6.67 ‰. However, their mean $\delta^{15}N$ value was 7.57 ‰, which is 0.90 ‰ greater than predicted, confirming that humpback whales in this study are likely to be incorporating fish into their diet to elevate the bulk $\delta^{15}N$ value in their tissue, which is also supported by the Bayesian modelling output presented above. Assuming a fish–whale TDF of 2.82 (after Borrell et al. 2012), then the 0.90 ‰ increase of measured versus predicted $\delta^{15}N$ value for whales represents 0.32 of a TP (0.90/2.82). If whales consumed a pure krill diet, then their expected TP would be 3.00. The mean TP of these humpback whales is therefore likely to be 3.32. The same calculation was carried out for the 2 whale clusters (A and B), for all females and for all males. Cluster A had a mean TP of 3.25, whilst the Cluster B mean TP was 3.76. Female mean TP was 3.23, and male mean TP was 3.43 (Table 1).

3.6.2. Modelled 'tRophicPosition' calculation

The 'tRophicPosition' model of Quezada-Romegialli et al. (2018) gave humpback whale mean TP estimates of 3.07 using the Borrell TDF (Table 1). The

Table 1. Trophic position (TP) estimates using 3 different methods of TP calculation for humpback whales *Megaptera novaeangliae*. The 'tRophicPosition' model was run applying trophic discrimination factors of Borrell et al. (2012), using Antarctic krill *Euphausia superba* as the nitrogen stable isotope baseline. TP estimates are shown as the median with 95% confidence levels (CL). The whole data set was used for the simple mathematical calculation and the 'tRophicPosition' model, whilst a subset of samples (n = 14) was used for the compound-specific stable isotope analysis (CSIA) calculations as indicated

Whale groups	TP calculation method		
	Simple arithmetic	'tRophic-Position' model	CSIA
All (n = 65, CSIA n = 14)			
Mean	3.32	3.07	3.33
Lower 95% CL		2.99	
Median		3.07	
Upper 95% CL		3.15	
Females (n = 35, CSIA n = 6)			
Mean	3.23	2.98	3.00
Lower 95% CL		2.89	
Median		2.98	
Upper 95% CL		3.06	
Males (n = 30, CSIA n = 8)			
Mean	3.43	3.18	3.57
Lower 95% CL		3.08	
Median		3.18	
Upper 95% CL		3.28	
Cluster A (n = 56, CSIA n = 9)			
Mean	3.25	3.00	3.14
Lower 95% CL		2.94	
Median		3.00	
Upper 95% CL		3.06	
Cluster B (n = 9, CSIA n = 5)			
Mean	3.76	3.51	3.67
Lower 95% CL		3.36	
Median		3.51	
Upper 95% CL		3.67	

female mean TP value was 2.98 compared to the male value of 3.18. Bayesian modelling posterior pairwise comparisons gave a probability of 99.8% that males had higher TP than females. The mean TP value of Cluster A was 3.00 compared to the Cluster B value of 3.51. Bayesian modelling posterior pairwise comparisons gave a probability of 100% that Cluster B whales had higher TP than Cluster A whales.

3.6.3. CSIA TP and TDF calculation

A biplot of $\delta^{15}N_{Glx}$ versus $\delta^{15}N_{Phe}$ values over trophic isoclines showed that male humpback whales

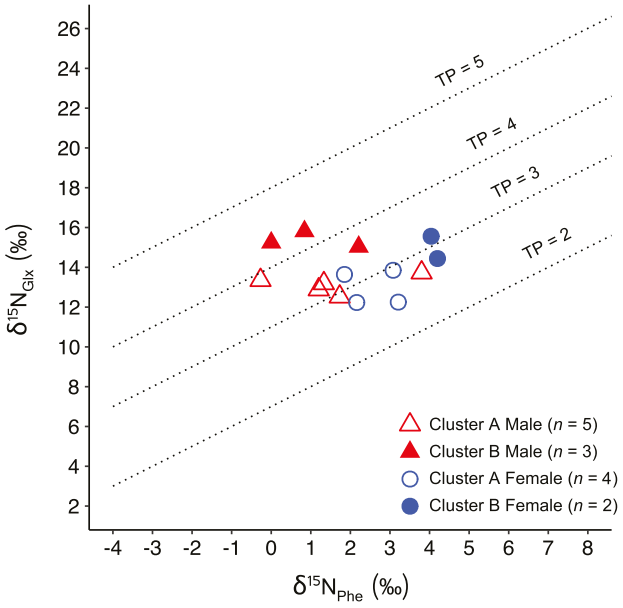

Fig. 8. Nitrogen stable isotope values of glutamic acid ('trophic amino acid', $\delta^{15}N_{Glx}$) plotted against phenylalanine values ('source amino acid', $\delta^{15}N_{Phe}$) for humpback whale *Megaptera novaeangliae* skin samples. Trophic isoclines with a slope of 1.0 and *y*-intercept intervals of 3.58 ‰ represent different trophic positions (TPs = 2, 3, 4 and 5). These isoclines are calculated according to the CSIA data-derived trophic discrimination factor of the whale: $TDF_{whale} = (Glx - Phe - 3.4)/(TP_{whale} - 1) = 3.58$, where TP_{whale} is 3.32 based on simple arithmetic TP calculation from bulk nitrogen stable isotope data (see Section 2.6 and Table S11)

generally had higher TP values than females, supporting the TP calculations presented above, with male TPs ranging from 2.82 to 4.23 compared to female values of 2.58 to 3.35 (Fig. 8; Table S2). Male mean TP values were 3.57, 0.53 compared to female mean TP values of 3.00, 0.28. Two male whales in Cluster B had the highest TP of above 4.20, with Cluster B whales having a mean TP of 3.67, 0.60, compared to whales in Cluster A with a mean TP of 3.14, 0.38. The mean TP of the subset of 14 whales analysed for CSIA was 3.33, 0.52.

3.6.4. Comparison of the three methods of TP calculation

The simple mathematical calculation using mean bulk $\delta^{15}N$ data from humpback whales and prey produced a mean whale TP of 3.32, which was very close to the CSIA-calculated value of 3.33, whilst the 'tRophicPosition' model produced a mean value of 3.07.

3.7. Isoscapes

When assigning whales to the most probable feeding locations based on comparisons between whale isotope data and isoscapes, the mean posterior probability density for the 56 whales in Cluster A was strongly bimodal when using only $\delta^{13}C$ data. This suggested that some individual Cluster A whales were feeding north of the BI, between ~53 and ~63° S between the Subantarctic Front and the Southern Antarctic Circumpolar Current Front (Fig. 1), whereas another subset was feeding further south along the edge of and within the RS at ~75° S latitude (Fig. 9a). When using both $\delta^{13}C$ and $\delta^{15}N$ values for the Cluster A whale assignments, the mean posterior probability was multi-modal: the density was much greater for regions around the RS, with lower density assignments between ~61 and ~67° S around the BI and just

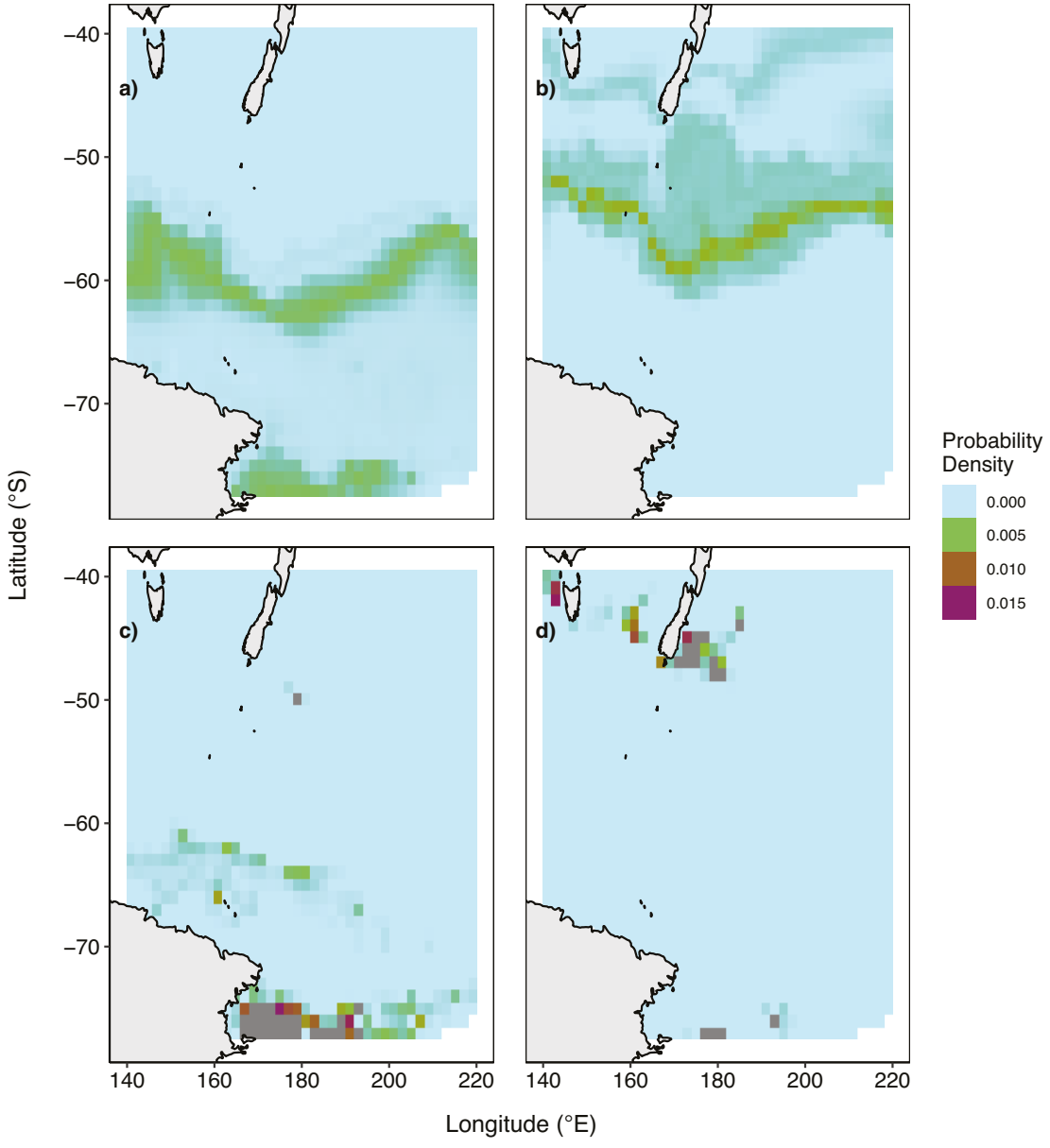

Fig. 9. Mean posterior probability densities for spatial assignment (cf. Wunder 2010) of individual humpback whale *Megaptera novaeangliae* foraging areas using spatial models (isoscapes) for $\delta^{13}C$ and $\delta^{15}N$ in suspended particulate organic matter of the Southern Ocean (St John Glew & Espinasse et al. 2021). (a,b) Assignments for Cluster A and B whales, respectively, using only $\delta^{13}C$ data; (c,d) assignments for Cluster A and B whales, respectively, using both $\delta^{13}C$ and $\delta^{15}N$ values. Posterior probability densities for the spatial assignment of individual Cluster B humpback whale foraging regions are provided in Fig. S9

north of the islands within the Southern Antarctic Circumpolar Current Front, and a few assignments around 50° S to the south-east of New Zealand (Fig. 9c). The mean posterior probability density of assignments based on $\delta^{13}C$ values for the 9 whales in Cluster B, by contrast, suggested a more diffuse bimodal distribution that extended further north, from ~50 to ~60° S, with low probability density to the southwest and east of New Zealand (Fig. 9b). When using both $\delta^{13}C$ and $\delta^{15}N$ data for the Cluster B assignments, the mean posterior probability was still multi-modal; however, the density was much greater for regions off the south-western and south-eastern coasts of New Zealand and around Tasmania, with an additional lower-density mode along the edge of the RS (Fig. 9d; Fig. S9).

4. DISCUSSION

This study applied multiple stable isotope methods to better constrain and understand Southern Ocean humpback whale trophic ecology. The primary hypothesis that Southern Ocean humpback whales have a similar diet to northern hemisphere humpback whales, eating a mixed diet of fish and krill, was confirmed. The secondary hypothesis, that some of the male humpback whales (those in Cluster B) were feeding at higher trophic levels than the rest of the sampled males (those in Cluster A) and most females (Cluster A) was also validated.

4.1. Comparison of humpback whale bulk stable isotope values, TP and diet with other published studies

The 'tRophicPosition' model calculations gave results consistent with the simple arithmetic and CSIA TP estimates, providing confidence in these methods. To place the bulk isotope values, TP calculations and 'MixSIAR' dietary conclusions from this study in context, a literature review of baleen whale stable isotope and TP data and likely consumed prey was carried out (Table S12 in Supplement 2 at www.int-res.com/articles/suppl/m734p123_supp2.xlsx). Whilst it is acknowledged that there is no control or correction made for any variability in $\delta^{15}N$ baselines for the data collated in the table, there are some interesting general trends. For example, for whales sampled in similar locations, whales that fed mainly on zooplankton generally had lower $\delta^{15}N$ values compared to whales sampled in the same area feeding predominantly on fish.

4.1.1. Southern hemisphere humpback whale $\delta^{15}N$ values

The mean humpback whale $\delta^{15}N$ value of 7.5, 0.7 ‰ from this study was relatively close to Southern Ocean humpback whale supplementary feeders of the E1 breeding stock sampled off east Australia (7.1, 1.0 ‰), feeding on Antarctic krill and Antarctic or temperate fish (Eisenmann et al. 2016). It was slightly higher than the mean value of 6.8, 0.4 ‰ reported for the E1 breeding stock (J. Groß unpubl. data), but close to the mean values measured for Population D (7.1, 0.5 ‰) and E2 (7.3, 0.5 ‰) in the same study (see Table S12 for descriptions of whale breeding stocks). Bengtson Nash et al. (2018) obtained $\delta^{15}N$ values closely aligned to this study for humpback whales sampled off Moreton Bay, south-east Queensland, Australia, with values ranging from 7.8, 1.2 ‰ for males to 7.4, 1.6 ‰ for females, reported as eating Antarctic krill. They too observed higher values for males than females. Owen et al. (2024) recorded $\delta^{15}N$ values of 7.4, 0.2 ‰ to 8.0, 0.1 ‰ for whales sampled off south-east Australia in the sub-tropics. In contrast, whales sampled in temperate waters off south-east Australia, observed to be eating temperate krill *Nyctiphanes australis* and pilchards *Sardinops sagax*, had higher values of 8.1, 0.2 ‰ to 9.2, 0.2 ‰ (Owen et al. 2024). Southern Ocean whales reported as being exclusive Antarctic krill 'classical feeders' of the D breeding stock had lower $\delta^{15}N$ values of 5.4, 0.7 ‰, and 'classical feeders' of the E1 breeding stock had values of 6.0, 0.7 ‰ (Eisenmann et al. 2016). These whales, which feed purely on Antarctic krill, had $\delta^{15}N$ values that were 1–2 ‰ lower than whales in the same study that were supplementing their diet with fish, and were between 1.5 and 2 ‰ lower than whales sampled around the BI in this study. These comparisons provide confidence in the Borrell 'MixSIAR' modelling results, which indicated that the Southern Ocean humpback whales of this study had substantial contributions of fish in their diet (posterior means: Cluster A 27%; Cluster B 35%). These proportions are plausible in the context of $\delta^{15}N$ values and dietary information from other studies presented in Table S12.

4.1.2. Comparison of Southern Ocean and northern hemisphere humpback whale $\delta^{15}N$ values

The wide range of $\delta^{15}N$ values reported for northern hemisphere humpback whales (Table S12) suggests that these whales are flexible generalists, feeding across multiple trophic levels or varying isotopic

baselines (Christensen et al. 1992, Filatova et al. 2013, MacKenzie et al. 2022). North-west Atlantic humpback whales (Gavrilchuk et al. 2014) and North Pacific Ocean humpback whales (Witteveen et al. 2008, 2009b, 2011, Fleming & Jackson 2011, Filatova et al. 2013, Wright et al. 2015, 2016), which consume a high proportion of fish in their diet, have much higher $\delta^{15}N$ values (13.0–14.7 ‰) than southern hemisphere humpback whales. This prevails even for those whales reported as predominantly eating krill, with some fish contributing to their diet (e.g. $\delta^{15}N$ values of 12.3–13.1 ‰: Fleming & Jackson 2011, Witteveen et al. 2011, MacKenzie et al. 2022). These $\delta^{15}N$ values are around 5 ‰ higher than Southern Ocean humpback whales in our study, thought to have a similar diet. This difference is likely driven by higher nitrogen stable isotope baseline values in northern hemisphere oceanic regions where whales were feeding compared to Southern Ocean feeding areas, in addition to potentially higher percentage fish contributions to the whales' diet. Mechanistic models of $\delta^{15}N$ baseline values in Somes et al. (2010) give values of 2–4 ‰ in the North Pacific Ocean and 4–8 ‰ in the north-east Pacific Ocean, whereas Southern Ocean spatial statistical models of compiled, measured $\delta^{15}N$ data suggest baseline values of 0–2 ‰ (Somes et al. 2010) and −3 to 2 ‰ (St John Glew & Espinasse et al. 2021). Mean SPOM $\delta^{15}N$ values measured in this study (Table S1) ranged from 0.1 to 1.5 ‰, which were considerably lower than northern hemisphere values given by Somes et al. (2010) and could explain the lower southern hemisphere $\delta^{15}N$ values of humpback whales.

4.1.3. Nitrogen stable isotope values and diets of other baleen whale species

Like humpback whales, fin whales have diets that range from almost exclusively foraging on copepods and krill, to supplementation of zooplankton with fish. Various studies of northern hemisphere fin whales report $\delta^{15}N$ values ranging from around 9.5–11 ‰ for whales with a predominantly zooplankton diet (Aguilar et al. 2014, Silva et al. 2019, MacKenzie et al. 2022), to 12–15 ‰ for fin whales that have fish in their diet (Gendron et al. 2001, Gavrilchuk et al. 2014, Ryan et al. 2014, Witteveen & Wynne 2016, Wild et al. 2018). Northern hemisphere blue whales *Balaenoptera musculus*, feeding exclusively on zooplankton, have $\delta^{15}N$ values ranging from 9 to 10 ‰ (Ostrom et al. 1993, Gavrilchuk et al. 2014, Silva et al. 2019, MacKenzie et al. 2022). These values for northern hemisphere fin and blue whales with pure zooplankton diets are around 1.5 ‰ higher than values for the Southern Ocean humpback whales in this study, shown to have a mixed diet of zooplankton and fish. A Southern Ocean blue whale skin biopsy obtained from the 2015 voyage had a $\delta^{15}N$ value of 6.9 ‰ (Table S12; S. Bury unpubl. data) which was 2–3 ‰ lower than northern hemisphere blue whale values. Although it is only a single blue whale $\delta^{15}N$ value, this measurement lends support to the concept that higher nitrogen stable isotope baseline values in the northern hemisphere oceans drive up the $\delta^{15}N$ values of whales feeding in those areas. The humpback whale mean $\delta^{15}N$ value of this study was 0.6 ‰ higher than the 2015 blue whale skin value, likely indicating that most of this study's humpback whales were feeding at a higher trophic level than blue whales, further supporting fish being a marked component of the humpback whale diet.

4.1.4. TP comparison of southern and northern hemisphere humpback whales

The mean simple arithmetic and CSIA TP values of 3.3, and the 'tRophicPosition' Borrell model value of 3.1 for humpback whales in this study (Table 1) agree with other published Southern Ocean humpback whale TP estimates (Table S12). For southern hemisphere whales, J. Groß (unpubl. data) calculated a mean TP of 3.0, 0.1 for the E1 humpback whale population, and a value of 3.1, 0.1 for the E2 population, which, from fatty acid concentration data, suggested that these whales included some higher TP prey in their diet. Haro et al. (2020) derived a TP of 3.4 from an ecosystem model for south-east Pacific humpback whales in the Magellan Strait.

In contrast, in the northern hemisphere, North Pacific Ocean humpback whales eating a diet of predominantly zooplankton and fish had TP values of between 3.1 and 3.3 (Hirons 2001, Witteveen et al. 2011, Wright et al. 2015, 2016). North Pacific Ocean humpback whales from the northern Gulf of Alaska that predominantly ate fish had a higher TP of 3.7 (Hirons 2001, Witteveen et al. 2008, 2011, Wright et al. 2015), whilst whales sampled from California to southern British Columbia with a similarly high fish content in their diet had a mean TP of 3.9 (Miller 2006, Witteveen et al. 2011). Pauly et al. (1998) used stomach content analysis to derive a mean TP value of 3.6 for humpback whales from a variety of northern hemisphere locations estimating a diet of 55% zooplankton and 45% fish, which is in line with the 3.7 TP value

for Cluster B whales in this study consuming a posterior mean of 34% fish estimated from the 'MixSIAR' Borrell model. A high TP value of 4.1 was assigned to European Arctic humpback whales by MacKenzie et al. (2022), who reported whales consuming a diet of euphausiids and fish. The highest value of 4.5 was reported by Ostrom et al. (1993) for humpback whales feeding off the coast of Newfoundland, Canada, consuming a diet of zooplankton, euphausiids, crustaceans, small fish and small squid, with squid likely elevating the TP of these whales.

4.1.5. TP and diet of other baleen whale species

Interestingly, fin whales consuming a similar diet to Southern Ocean humpback whales had TP values similar to the value of 3.3 determined in this study (TP 3.4: Pauly et al. 1998; TP 3.0: MacKenzie et al. 2022). The higher fin whale TP value of 4.5 reported by Haro et al. (2020) for whales feeding in the Magellan Strait off Chile can be explained by a diet of higher trophic level organisms including fish and cephalopods. Blue whale TP values ranged from 3.0 (MacKenzie et al. 2022) to 3.2 (Ostrom et al. 1993, Pauly et al. 1998), being slightly lower than the TP of whales in our study. These TP comparisons provide further evidence that the Southern Ocean humpback whales in our study were consuming a diet predominantly of zooplankton, supplemented with varying proportions of fish.

4.2. Isotopic niche space and diet of Cluster A and B humpback whales

An organism's isotopic niche space provides insight into its ecological range, resource use and geographical diversity, where niche parameters can respond rapidly to changes in prey abundance and intra- and interspecific competition (Bearhop et al. 2004, Newsome et al. 2007, Fry & Davis 2015). The smaller isotopic niche area of Cluster A compared to Cluster B whales in this study suggested that Cluster B individuals might be more specialised, have more similar ecological behaviour and be more vulnerable to change (Newsome et al. 2012). The higher isotopic values and TP of males and Cluster B whales compared to females suggested that the former were either feeding at a higher trophic level or in areas where baseline $\delta^{15}N$ values were elevated. The CSIA 'flat' trend line for $\delta^{15}N_{Phe}$, which remained relatively constant with increasing bulk $\delta^{15}N$ values, indicated that the elevated $\delta^{15}N$ values of male and Cluster B humpback whales were most likely due to trophic influences, rather than isotopic baseline effects. In addition, $\delta^{15}N$ values of threonine were generally higher for Cluster B than Cluster A whales, suggesting that Cluster B whales foraged at a higher trophic level (Lübcker et al. 2020).

4.3. Feeding locations of the whales

There was good agreement on feeding locations of the humpback whales surmised from the 'MixSIAR' modelling data and from the isoscape-based whale feeding location assignments. 'MixSIAR' modelling data indicated that Cluster B whales likely fed closer to the highly productive BI than along the RSS and in the RS, feeding on more fish than Cluster A whales, whilst Cluster A whales fed mostly in the RSS and RS area. In both cases, whales consumed varying but sometimes high proportions of fish (2–60%), contrary to the paradigm of them being exclusive krill feeders (Chittleborough 1965, Bannister & Hedley 2001, Waugh et al. 2012). These data are consistent with more recent observations that Southern Ocean humpback whales consume fish as part of their diet during migration (Eisenmann 2016, Groß et al. 2020, Owen et al. 2024) and that they are seemingly quite plastic in their feeding behaviour (Gavrilchuk et al. 2014, Haro et al. 2016).

The strong latitudinal gradient of SPOM $\delta^{13}C$ values (Fig. 10), enabled the feeding areas of Cluster A and B whales to be estimated using the isoscape-based whale assignment method (Wunder 2010, St John Glew & Espinasse et al. 2021). From the $\delta^{13}C$ and $\delta^{15}N$ assignments, Cluster A and B whales likely fed in different locations: Cluster A whales probably fed further south, mainly in the RSS and RS region with lower density assignments around and to the north of the BI, whilst Cluster B whales seem to have predominantly fed south-east of Australia and south-west and south-east of New Zealand, with 1 or 2 individuals assigned to the RS.

The assignments using both $\delta^{13}C$ and $\delta^{15}N$ data (Fig. 9c,d) produced results that seem more plausible than assignments using only $\delta^{13}C$ data (Fig. 9a,b). This is likely because the field-measured $\delta^{15}N$ SPOM values more closely matched those predicted by the $\delta^{15}N$ isoscape model, than the equivalent field- and isoscape-modelled $\delta^{13}C$ values (Fig. 10; Fig. S10). Trends in measured SPOM $\delta^{13}C$ values (Transect SPOM) and modelled data from the St John Glew & Espinasse et al. (2021) isoscape with latitude were

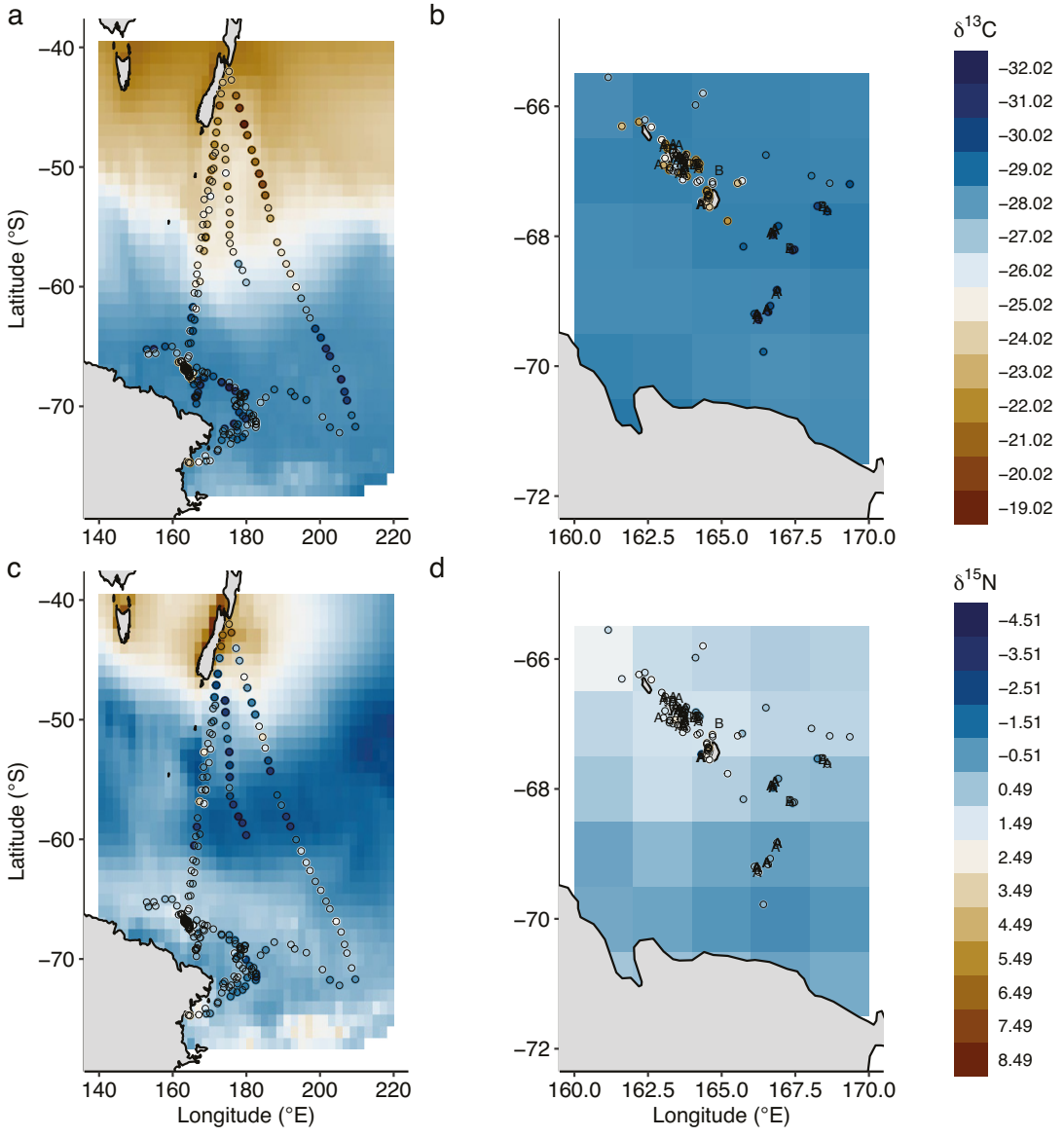

Fig. 10. Southern Ocean spatial variability of (a) $\delta^{13}C$ and (c) $\delta^{15}N$ values of suspended particulate organic material (SPOM) derived from the isoscapes model of St John Glew & Espinasse et al. (2021) (baseline map) and field-measured SPOM $\delta^{13}C$ and $\delta^{15}N$ values (filled circles). (b) $\delta^{13}C$ and (d) $\delta^{15}N$ modelled isoscape for SPOM and field data for the regional area around the Balleny Islands. The letters A and B in panels b and d indicate the locations of Cluster A and Cluster B whales when skin biopsies were sampled

quite closely aligned between 40 and 60° S (Fig. 11). However, there were clear anomalies, which likely reflect localised regional variability in baseline $\delta^{13}C$ values due to enhanced primary productivity within the Subantarctic Front, Polar Front and Southern Antarctic Circumpolar Current Front regions, areas of enhanced upwelling, such as around the BI, and the ice-melt regions of the RSS and RS. These small-scale, high-productivity areas, such as around the BI and other localised highly productive frontal regions, are not captured in large-scale spatial modelling (such as St John Glew & Espinasse et al. 2021).

The elevated $\delta^{13}C$ values of Cluster B whales indicate that these whales were either predominantly feeding (1) further north than the other whales; (2) in more productive waters and/or closer inshore; (3) on benthic or ice-associated fauna; or (4) off the shores of eastern Australia or New Zealand during migration. The assignment results support (1) and (4), but (2) and (3) could be equally plausible explanations. During the whale sampling periods in 2010 and 2015, high productivity around the BI produced locally high $\delta^{13}C$ phytoplankton values and large swarms of krill and silverfish (O'Driscoll & Double 2015, Harrison et al.

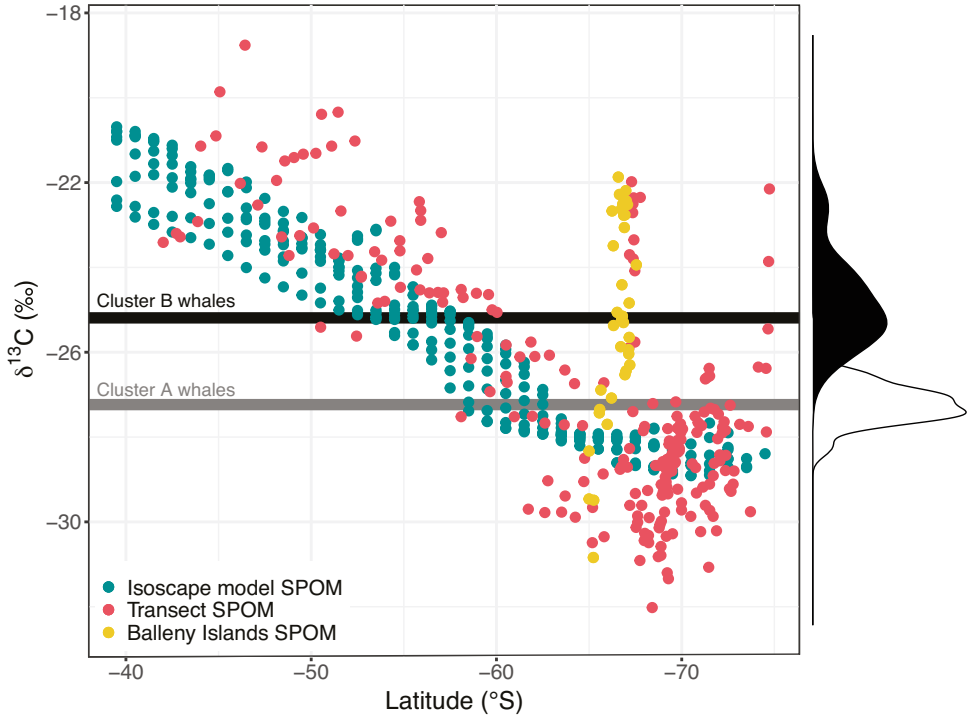

Fig. 11. Variation in $\delta^{13}C$ values of surface suspended particulate organic matter (SPOM) with latitude. 'Isoscape model SPOM' are the 'no interactions' modelled SPOM isoscape values from St John Glew & Espinasse et al. (2021); 'Transect SPOM' are field-measured $\delta^{13}C$ SPOM values from 2010 and 2015 voyages on transects from New Zealand to the Ross Sea; 'Balleny Islands SPOM' are $\delta^{13}C$ SPOM data from the same voyages measured in the vicinity of the Balleny Islands. The $\delta^{13}C$ trophic discrimination factor of Borrell et al. (2012) was subtracted from all plotted humpback whale *Megaptera novaeangliae* skin values to enable comparison to SPOM $\delta^{13}C$ data: the grey and black solid lines are the median $\delta^{13}C$ values for Cluster A and B whales, respectively. The white and black histograms are the frequency distributions of $\delta^{13}C$ values for Cluster A and B whales, respectively

2020). Observational data (Gales 2010) shows that the BI is an important feeding ground for Southern Ocean humpback whales that primarily originate from east Australia (Constantine et al. 2012, Andrews-Goff et al. 2018), and the data from our study support this.

Cetacean distributions generally reflect patterns of oceanographic processes, such as fronts, generating regional biological activity (Bost et al. 2009, Riekkola et al. 2019). Southern Ocean humpback whales have been observed to largely feed along the marginal ice zone, the RSS and slope, and seamount/island areas characterised by local hotspots of productivity (Kaschner 2008, Bestley et al. 2019, Harrison et al. 2020). Seamounts and plateaus represent key feeding areas for cetaceans (Johnston et al. 2008, Skov et al. 2008, Morato et al. 2010) and are important for the New Caledonia humpback whale breeding stock and the E1 population (Garrigue et al. 2015) and Western Australian humpback whales, which also feed along the western boundary current (Bestley et al. 2019). Surface waters around oceanic islands and plateaus often have high nutrient and iron concentrations due to upwelling effects (Blain et al. 2001, Schallenberg et al. 2018), high chlorophyll *a* concentrations (Sokolov & Rintoul 2007) and elevated primary productivity. These phenomena, collectively recognised as the Island Mass Effect (Doty & Oguri 1956, Blain et al. 2001), generate increased $\delta^{13}C$ and $\delta^{15}N$ SPOM values (Bidigare et al. 1997, Popp et al. 1998), resulting in higher isotopic values in humpback whales feeding in these areas.

Key predictors of foraging behaviour are water temperature (Owen et al. 2019), distance from the ice edge, ice melt rate and variability in ice concentration 2 mo prior to arrival on the feeding grounds (Nicol et al. 2008, Andrews-Goff et al. 2018, Riekkola et al. 2019). Humpback whale feeding is thus sustained by a biological cascade, in which new biological productivity is triggered by ice melting, which in turn supports phytoplankton grazers such as krill and other zooplankton, and ultimately whales. Humpback whales can show persistent space use and site fidelity (Tynan 1998, Branch 2011, Bombosch et al. 2014), with whales moving through the same location or occupying adjacent habitats over consecutive austral summers (Andrews-Goff et al. 2018). The similarity between 2010 and 2015 whale skin isotopic values in this study supports this observation.

4.4. Potential factors affecting stable isotope values of Southern Ocean humpback whales

4.4.1. Whale sex and pregnancy

Although this study found no isotopic difference between humpback whale age groups, sampling location or year, males had slightly higher $\delta^{13}C$ and $\delta^{15}N$ values than females. Several studies of humpback whales have found no difference in $\delta^{13}C$ or $\delta^{15}N$ values between sexes (Witteveen et al. 2011, Gavrilchuk et al. 2014, Fleming et al. 2016, Bengtson Nash et al. 2018). In addition, a study of southern hemisphere humpback whale blubber fatty acid profiles showed no clear nutritional status separation between females and males (Eisenmann 2016). The mean isotopic difference between males and females in this study was not large (Tables S2 & S7) and may be due to a small subset of male whales feeding at a higher trophic level (Fig. 4; Fig. S4). However, there are other factors that should also be considered.

Differences in size, time spent on feeding grounds and associated fasting duration between male and female humpback whales, plus the reproductive status of females, could contribute to the isotopic difference in their skin tissues superimposed on diet effects. Adult female humpback whales range in length from 12 to 17 m and are between 40 and 150 cm longer than males. Considering the potential positive relationship between size and $\delta^{15}N$ values (Jennings et al. 2002, 2008), one might expect higher $\delta^{15}N$ values in females than males. Unfortunately, there were no size-based data within this study to assess if size had any effect on stable isotope ratios. Movement modelling studies of humpback whales migrating from Western Australia to the Southern Ocean showed that females moved faster than males during resident and transit periods, which Bestley et al. (2019) attributed to either their larger size or different energetic requirements. A difference in metabolism and energetic requirements between males and females could also contribute to sex-related isotopic differences.

Pregnancy is also known to affect the stable isotope composition of females, such that their isotopic values do not exclusively reflect diet (Clark et al. 2016). Pregnant mammals often have lower $\delta^{15}N$ values as they become net anabolic (i.e. as they increase protein synthesis) and decrease the excretion of nitrogenous waste (Fuller et al. 2004, Martínez del Rio et al. 2009, Kurle et al. 2014). Carbon stable isotope values also decrease as pregnant females mobilise lipid stores to meet the energetic demands of pregnancy (Kelly 2000, Kurle & Worthy 2001). The existence and magnitude of these effects vary among species (Kurle 2002, Habran et al. 2010, Newsome et al. 2010). There was no information relating to the pregnancy status of females in this study. However, Southern Ocean humpback whale pregnancy rate estimates of 37% (Chittleborough 1965), 18–48% (Clark et al. 2016) and 30–86% (mean 52%) (Pallin et al. 2023) in the Western Antarctic Peninsula, and an estimate of 57% obtained from whales sampled around the Kermadec Islands (Riekkola et al. 2018), indicate that pregnancy could have accounted for the overall lower mean $\delta^{13}C$ and $\delta^{15}N$ values in females compared to males. For future studies, it would be useful to carry out progesterone analysis of biopsied blubber to obtain information on the proportion of pregnant females in the population. Without this information, pregnancy-related changes in stable isotope values are difficult to assess and complicate interpretations of data to infer diet and migration (Newsome et al. 2010, Clark et al. 2016).

4.4.2. Time spent on feeding grounds and feeding and fasting effects on whale stable isotope values

Another factor contributing to humpback whale isotopic variability is the length of time spent on the feeding grounds. Male and female humpback whales arrive at and depart from Antarctic feeding grounds at different times: the first whales to arrive from October onwards are pregnant females, then males, then lactating females with a calf, with whales departing around April in the order of lactating females with a calf, males, then pregnant females (Chittleborough 1965, Dawbin 1966, 1997). In addition, Riekkola et al. (2018) noted that Oceania humpback whales migrated to different feeding grounds based on their life history stages, with all tagged females with calves in their study migrating to the Ross Sea region. Some non-pregnant females also overwinter in Antarctica to improve body condition for the next reproductive cycle (Clark et al. 2016). For the whole population, if around 20–60% of whales are pregnant, then between approximately one-fifth and two-thirds of the females may arrive before males and the remaining proportion of females (those that are lactating) after the males.. Differences in arrival time may therefore not account for male/female differences in isotope values, since arrival times for males/females over the whole population could be averaged out to be quite similar; however, differences in arrival time could contribute to greater isotopic variability within the population.

Later arrival on the feeding grounds could mean that those whales spend a longer time migrating and fasting. Some studies have shown that fasting increases $\delta^{15}N$ values of some organisms by up to 1 ‰ (Hobson et al. 1993, Cherel et al. 2005a), due to protein synthesis using ^{15}N-enriched amino acids derived from catabolism of endogenous protein (Hatch 2012). Other studies, however, observed that $\delta^{15}N$ values declined during periods of reduced feeding, reflecting changing $\delta^{15}N$ baselines between summer and winter feeding grounds, rather than tissue metabolism effects (Matthews & Ferguson 2015, Pomerleau et al. 2018). Furthermore, several studies have suggested that $\delta^{15}N$ values are not affected by fasting (Hobson & Schell 1998, Ben David et al. 1999, Williams et al. 2007, Gómez-Campos et al. 2011, Aguilar et al. 2014, Owen et al. 2024). For humpback whales, this is likely because they have evolved to endure long predictable periods of fasting, so the effects of fasting are not equivalent (in terms of metabolic and biochemical processes) to starvation, i.e. they do not experience 'nutritional stress' during these times, due to physiological adaptation (Kempster et al. 2007, Witteveen et al. 2009a). In addition, Riekkola et al. (2020) surmised from humpback whale tracking and energetic studies that even extreme long-distance migration does not appear to adversely affect the energetic expenditure of these animals.

Blubber stores are likely to be the primary source of energy until stages of extreme nutritional stress are reached (Aguilar et al. 2014). This is because the quantity of lipid reserves stored by an organism influences the degree to which protein versus lipid is catabolised for energy (Elia et al. 1999). Large fat reserves mean the whales are less likely to metabolise ^{15}N-enriched proteins during fasting (Polischuk et al. 2001, Aguilar et al. 2014). Evidence to support minimal effects of fasting on $\delta^{15}N$ values is provided by Bengtson Nash et al. (2018), who sampled E1 breeding stock humpback whales off the south-east Queensland coast and measured very similar $\delta^{15}N$ values in southward-migrating 'fasting' whales (7.5, 1.3 ‰) compared to the northward migrating 'post-feeding' whales (7.7, 1.8 ‰). These southward-migrating 'fasting' whales not only had similar $\delta^{15}N$ values, but also similar $\delta^{13}C$ values (−24.9, 1.0 ‰) to humpback whales in our study, which had been feeding in Antarctica for several months ($\delta^{13}C$ −25.2, 1.0; $\delta^{15}N$ 7.6, 0.7). Owen et al. (2024) also noted that southward migrating whales in the subtropics had similar isotope values to whales feeding in the Antarctic, supporting the notion that there is little change in isotopic values due to whale fasting. Furthermore, alanine $\delta^{15}N$ values (which, if higher, are indicative of fasting: Lübcker et al. 2020) were similar between Cluster A and B whales, indicating fasting was likely not affecting nitrogen isotope values.

A further consideration is that delayed arrival on the feeding grounds could mean that those whales had more time for migratory feeding on fish and krill in temperate waters (Gales et al. 2009, Andrews-Goff et al. 2018, Owen et al. 2024), which would increase their $\delta^{15}N$ values. Stable isotope analysis of baleen whale plates showed that supplementary feeding may be a common strategy for about 30% of east Australian humpback whales (Eisenmann 2016). It is likely that the Cluster B whales with higher isotope values were late-arriving males engaged in feeding in temperate waters off south-east Australia or southern New Zealand during their southward migration while migrating en route to Antarctica (corroborated by the whale assignment locations in Fig. 9d and Fig. S9), supporting observations of Gales et al. (2009). This supplementary feeding whilst migrating may be an indicator that the Southern Ocean ecosystem does not meet the energetic requirements of the humpback whales during the summer feeding season, as suggested by Riekkola et al. (2018), or it could just be opportunistic feeding behaviour.

4.4.3. Effects of quality, abundance and location of prey on humpback whale stable isotope values

Humpback whales are largely opportunistic foragers that depend on quality, high-lipid-content, energy-dense prey to maximise fat deposition in their blubber layers, providing a sustained energy source (Worthy & Edwards 1990, Koopman et al. 2002, Witteveen et al. 2011). At low latitudes, humpback whales can lose between one-third to half of their body mass (Dawbin 1966, Lockyer 1981, Baraff et al. 1991) due to lipids being catabolised during migration and periods of limited nutrient intake (Lockyer 1986, Castellini & Rea 1992, Parrish 1997). As has been shown for other animals (Urton & Hobson 2005, Inger et al. 2006), prey choice for humpback whales can therefore significantly impact survival, migration and reproductive success (Witteveen et al. 2011). In addition, baleen whales need to feed on aggregated prey above a threshold density to ensure positive net energy gain from a feeding event (Piatt & Methven 1992, Hazen et al. 2009, Goldbogen et al. 2011). It is thus possible that the consumption of a higher-quality diet (McCutchan et al. 2003, Vanderklift & Ponsard 2003) was a contributor to the higher $\delta^{15}N$ values of Cluster B whales of this study.

As confirmed by this study, Southern Ocean humpback whales are dependent on Antarctic krill as a major dietary component. Krill are strongly associated with the sea ice extent and abundance of associated sea ice algae (Atkinson et al. 2004, Loeb et al. 1997) and are thus vulnerable to climate change (Flores et al. 2012). They are recruited at the sea ice edge and disperse northwards following sea ice melt (Ward et al. 1990, Brierley et al. 1999). Their abundance is dependent on high levels of primary productivity, which in turn is affected by ocean circulation, bathymetry, coastline morphology, localised upwelling and frontal dynamics (Bathmann et al. 1997, Strutton et al. 2000, Martinson et al. 2008). These factors, combined with climate change, exert important controls on isotopic baselines and prey availability for humpback whales (Gross 2005, Fountain et al. 2012, Pallin et al. 2023). Higher encounter rates of humpback whales tend to be observed in the northern RS (65–70° S), where this study was located, which is a region of rapid ice retreat and high chlorophyll productivity (Moore & Abbott 2000, Nicol et al. 2006). Clarke & Tyler (2008) observed that, whilst most postlarval Antarctic krill populate the upper 150 m of the water column, some can be found in abyssal waters as deep as 3500 m, where omnivory is increased with resultant higher $\delta^{15}N$ values (Cresswell et al. 2009, Bengtson Nash et al. 2018). This could explain the wide variability observed in krill $\delta^{15}N$ values in this study, ranging from 2.03 to 7.39 ‰ (Table S1), which is reflected up the food chain in myctophids and Antarctic silverfish.

Since there is lower abundance of Antarctic krill in the RS region compared to the Scotia Sea (Atkinson et al. 2004, 2017), it is likely that humpback whales feeding in the RS area have lower dependence on krill than those elsewhere in the Southern Ocean. Due to ocean acidification, a complete collapse of Antarctic krill populations is forecasted by 2300 if current CO_2 emissions are not mitigated (Kawaguchi et al. 2013). In this scenario, humpback whales may avoid the threat of starvation by being highly responsive to environmental oscillations through dietary diversification (Bengtson Nash et al. 2018). Diversity in the interannual feeding strategies of humpback whales from the eastern Australian E1 breeding stock demonstrates plasticity in prey selection and migratory behaviour of this species (Eisenmann et al. 2016), which provides hope for adaptive strategies and their long-term survival. The more diverse diet of Southern Ocean humpback whales confirmed by this study provides further evidence for possible dietary plasticity in the face of potential anthropogenically mediated changes to the trophic structure and prey abundance and distributions within the Southern Ocean.

Humpback whales in the north-east Pacific Ocean have shown temporal and geographical variability in diet driven by changes in prey abundance (Fleming et al. 2016). Changes at lower trophic levels are often amplified at higher trophic levels due to non-linear responses of biological communities and predatory interactions (Friedland et al. 2012, Stock et al. 2014). Such top-predator responses are due to the dynamic interactions and cumulative effects between changing oceanographic conditions, mid-trophic-level prey dynamics, and predator foraging behaviour (Hilty & Merenlender 2000, Abraham & Sydeman 2004, Sydeman et al. 2013). Although our data show an isotopic difference between males and females, this difference is not marked (< 1 ‰ between female and male mean values for both $\delta^{13}C$ and $\delta^{15}N$), with humpback whale stable isotope values primarily reflecting consumption of the dominant prey types in the ecosystem. Changes in prey abundance likely drive changes in whale diet at the population level (males and females combined), such that humpback whale prey composition can be an indicator of dominant prey types in the ecosystem (Fleming et al. 2016). Thus, multi-decadal changes in foraging behaviour of humpback whales could be a useful synoptic indicator of changing oceanographic and ecological conditions.

The variety and complexity of factors that can influence humpback whale $\delta^{13}C$ and $\delta^{15}N$ values makes it difficult to provide a definitive assessment of the relative importance of different drivers determining their isotopic composition. Additionally, biopsy collection could be affected by sampling biases, since animals that spend more time at the surface are more easily sighted and sampled and may therefore be overrepresented in the sampling. Cows with calves may be more readily sighted and sampled, as they are often more active at the surface than males or non-nursing females. Whales that spend less time at the surface and perhaps feed in deeper waters may be underrepresented, such that the full dietary range of isotopic values is not captured by biopsy sampling. Nonetheless, dietary intake and feeding location are likely to be the dominant determinants of stable isotope values, with other factors potentially also contributing to isotopic variation.

5. CONCLUSIONS

This study combined multiple stable isotope methods to quantify diet and TP and to identify

foraging areas of Southern Ocean humpback whales. It confirmed the hypothesis that Southern Ocean humpback whales sampled around the BI and in the RS had a mixed diet of plankton, krill and fish, similar to the diet of northern hemisphere humpback whales. The percentage of fish consumed varied (2–60%), but proportions were often high, thus challenging the widely held paradigm of Southern Ocean humpback whales being exclusive krill feeders and re-enforcing the notion that they have dietary plasticity. Southern Ocean humpback whales had lower $\delta^{15}N$ values than northern hemisphere populations and lower TP values, likely due to a combination of lower baseline $\delta^{15}N$ surface water values in the Southern Ocean compared to the northern hemisphere and a lower percentage consumption of fish, respectively.

'MixSIAR' prey apportionment modelling and TP calculations using the TDF of Borrell et al. (2012) produced data that closely aligned with trophic information from other studies, hence placing more confidence in the Borrell et al. (2012) factors than the Post (2002) values. It is recommended that future studies of humpback whale trophic ecology utilise the TDFs of Borrell et al. (2012).

The majority of the whales sampled in this study appeared to be foraging in the RS, along the RSS and in the vicinity of the BI. An isotopically distinct subset of male humpback whales with higher TP was identified through bulk carbon and nitrogen and CSIA of N-AA. Isoscape-based whale assignments combined with regional isotopic baseline field measurements indicated that these whales were either taking higher-quality food sourced from productivity hotspots such as the BI and/or frontal upwelling areas, or that they had fed en route to Antarctica in temperate waters off south-eastern Australia, south-west or south-east New Zealand.

Since Antarctic ecosystems are particularly vulnerable to climate change, warming, freshening, ocean acidification and shifts in primary production patterns leading to variable krill abundance, an improved understanding of ocean biogeochemistry and trophic interactions is becoming increasingly important, both for predicting change and for robust ecosystem management of the Ross Sea region. It is hoped that the development of seasonal and regional smaller-scale isoscapes combined with improvements in remote sensing techniques and oceanic modelling will enhance the applicability of stable isotope tools to better understand and manage such ecosystems. As demonstrated by this study, *in situ* field data are essential to inform and rationalise these models to improve data interpretations, and to assist managerial decisions and policy implementation to better protect and conserve Southern Ocean humpback whales and their environment, particularly within the Ross Sea region marine protected area. The revelation of a more diverse Southern Ocean humpback whale diet has implications for predicting the impact of future ecosystem changes on the foraging and hence breeding success of humpback whales. It also highlights the need for further dietary studies on other marine predators in the Southern Ocean that are thought to be highly dependent on Antarctic krill.

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