Historical Niche Partitioning of Baleen Whales in the Western South Atlantic

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ABSTRACT

Baleen whales are key marine predators that were heavily exploited throughout the 20th century, resulting in reductions in population size for many species. Whilst population recovery is evident for some species, baseline information on ecological niches is still unknown, rendering it hard to forecast the manner in which baleen whales will reoccupy their former ecological niches as they recover. Biogeochemical analyses of bone fragments from 20th century whaling provide invaluable information on the foraging ecology and trophic niches of whale populations in the past, and provide a baseline for assessing recovery. Here, we combine ZooMS and DNA barcoding to assign bone specimens to species from three former whaling sites in the western South Atlantic, and use stable isotope analysis of carbon and nitrogen to infer differences in the long-term foraging preferences of baleen whales utilising western South Atlantic feeding grounds. These datasets indicate that baleen whale species partitioned prey resources with slight overlap in isotopic niches for three of the four species, with sei whales likely to be foraging predominantly on different feeding grounds relative to Antarctic blue, fin and humpback whales. Niche sizes reveal that Antarctic blue and sei whales are specialist feeders, at the population-level, suggesting that they are less likely to adapt to continuing climate change relative to more generalist fin and humpback whales. Characterising historical foraging baselines such as these are essential for assessing the ecological implications of changing oceans for recovering whale populations.

KEYWORDS

Baleen whale, resource partitioning, Stable Isotope Analysis, Peptide fingerprinting, South Atlantic, foraging ecology

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1. INTRODUCTION

Forecasting population change is essential to ocean management, particularly as climate change drives dramatic shifts in marine ecosystems worldwide (Fordham et al. 2013, Hattab et al. 2016, Turvey & Crees 2019, Franco et al. 2020). Exploitative harvesting practices have resulted in biodiversity declines and abundance reductions for many species (Pauly et al. 2005, Kaschner et al. 2011, Pimiento et al. 2017, Pacoureau et al. 2021). Projecting anticipated fluctuations in population dynamics provides the key to prevent further declines and enable stakeholders to develop mitigation strategies to preserve and protect biodiversity and ecosystem health (Tulloch et al. 2020, Cheung et al. 2022, Ghisbain et al. 2023).

Understanding predatory guilds and their prey preferences is essential for predicting population dynamics under changing environmental conditions (Hattab et al. 2016, Bourdaud et al. 2021). Specialists have decreased capacity to adapt to environmental change compared to generalists, so measures of niche speciality are essential to prioritise species of conservation concern (Gilchrist 1995, Monaco et al. 2020). For example, pelagic seabirds with specialist diets and slow reproductive rates have been shown to have heightened vulnerability to extinction under climate change relative to seabirds with fast reproductive rates and varied diets, even when these faster-life history species have narrower habitat breadths (Richards et al. 2021). Metrics of niche specialisation alongside an understanding of food web dynamics is crucial for early warning signs of extinction vulnerability and species conservation prioritisation.

Competitive exclusion principle (CEP) ecological theory states that in a scenario where two species occupy the same ecological niche, one species will always out-compete the other (Hardin 1960), often resulting in the partitioning of resources between sympatric species (e.g. Polito et al. 2015, Petalas et al. 2021, Buss et al. 2022); although there are some exceptions to the rule (e.g. Soininen et al. 2015, Bachiller & Irigoien 2015). Marine species partition resources in a multitude of ways, including but not exclusive to: prey size (Santora et al. 2010); taxon (Croxall et al. 1997); foraging depth (Herr et al. 2016, McCarthy et al. 2021); time of day (Lear et al. 2021); seasonality (Fossette et al. 2017); locality (Thiebot et al. 2012), or combinations of these strategies.

In the Southern Hemisphere, several baleen whale species migrate to higher latitude feeding grounds in spring, primarily feeding on large aggregations of krill in Antarctic and sub-Antarctic waters (Mackintosh & Wheeler 1929, Mackintosh 1946, Brown 1968, Kawamura 1980, Ichii & Kato 1991, Friedlaender et al. 2009, 2021, Herr et al. 2016, Mikhalev 2020, Savoca et al. 2021). At the Antarctic Peninsula, for instance, Antarctic krill (*Euphausia* *superba*) dominate the food web and serve as a crucial prey item for many species. This coexistence of multiple species feeding on the same prey appears inconsistent with the Competitive Exclusion Principle (CEP). However, partitioning of resources is evident, with different whale species utilising shared prey resources in distinct ways—foraging at different proximities to coastal areas, across different latitudes, at varied depths, or during different times of the year (Friedlaender et al. 2009, 2021, Herr et al. 2016), thus supporting the CEP.

During the early 20th century, unsustainable exploitation led to dramatic declines in baleen whale populations in the Southern Hemisphere and across the Antarctic and sub-Antarctic regions (Rocha et al. 2015) with consequences for local marine ecosystems (Roman & McCarthy 2010, Roman et al. 2014). Many Southern Hemisphere whale populations are now recovering, albeit during a period of environmental change (Whitehouse et al. 2008, Aronson et al. 2011, Flores et al. 2012, Trathan et al. 2012). Warming sea temperatures have resulted in a southward contraction of *E. superba*, and substantial changes in regional sea ice extents have been observed (Atkinson et al. 2019, Fogt et al. 2022, Turner et al. 2022). Past whale declines and subsequent recovery, coupled with continuing environmental changes due to rising global temperatures, are likely to result in alterations to energy flow and primary productivity in these ecosystems (Croll et al. 2006, Essington 2007, Trathan & Reid 2009, Morissette et al. 2012).

To fully understand how whale declines and recovery will integrate with environmental change, a good understanding of whale resource use and partitioning is required. Estimating this dynamic is challenging as dietary studies in this region are few and have predominantly focused on humpback whale, *Megaptera novaeangliae*, and Antarctic minke whale, *Balaenoptera bonaerensis* (Ichii & Kato 1991, Friedlaender et al. 2009, Das et al. 2017, Bengtson Nash et al. 2018, Uchida et al. 2021). Four rorqual species (Antarctic blue whale, *Balaenoptera musculus subsp. intermedia*; fin whale, *B.physalus*, humpback whale, *Megaptera novaeangliae*, and sei whale, *B.borealis*) were heavily hunted during the early 1900s (Rocha et al. 2015). In the western South Atlantic, all four species were historically caught by whalers in high numbers at sub-Antarctic and/or Antarctic latitudes with whale bones discarded at ex-whaling sites (Mackintosh 1946, Headland 1992, Sremba et al. 2015, Buss 2022). Population genetics and movement ecology studies suggest that a single breeding population for each of these species spans the western South Atlantic Humpback whales that have genetically distinct breeding grounds around the Southern Hemisphere form Breeding group ‘A’ in the western South Atlantic (Rosenbaum et al. 2017). This population winter off Brazil and have been satellite tracked foraging at high latitudes, predominantly near to South Georgia and the South Sandwich Islands ((Zerbini et al. 2019), and references therein). Sei whales have been observed migrating between Brazil and the Falkland Islands/Islas Malvinas (hereafter referred to as the Falkland Islands) where they feed in coastal waters between summer and autumn (Weir et al. 2019, 2020), however, Southern Hemisphere population structuring and connectivity is poorly understood (Pérez-Álvarez et al. 2021, Buss 2022). Fin whales and Antarctic blue whales are commonly observed feeding at high latitudes (Jackson et al. 2020, Calderan et al. 2020, Viquerat et al. 2022, Herr et al. 2022), population structure is poorly understood in the South Atlantic, and no genetic evidence has identified longitudinal population structuring within the Southern Hemisphere to date (Sremba et al. 2012, 2023, Attard et al. 2016, Pérez-Alvarez et al. 2021, Pérez-Álvarez et al. 2021, Buss 2022, Buss et al. 2023).

Dietary analysis of stomach contents or faeces is often used to determine prey choice of marine predators (Flinn et al. 2002, Branch et al. 2007). However, faecal samples are challenging to obtain *in situ* across the high seas, and since the whaling moratorium in 1986, stomach contents are only occasionally collected opportunistically during infrequent stranding events (e.g., Lick & Piatkowski 1998, Meynier et al. 2008). Instead, carbon and nitrogen isotope analysis of proteinaceous tissues can be used to infer the ecological niches of organisms and quantify niche partitioning between groups of marine predators (Matich et al. 2017, Malinowski et al. 2019, Galindo et al. 2021). Indeed, this technique has been utilised on skin biopsies of cetaceans for several decades (Todd et al. 1997, Wild et al. 2018, Milmann et al. 2020, Troina et al. 2021). In these studies the foraging niche is often inferred from the multi-dimensional isotopic niche space, whereby the bivariate (or sometimes multivariate) distribution of stable isotopes (predominantly carbon and nitrogen), measured from bone collagen, skin or keratinous tissues (e.g., hair, feather, nails, baleen), are used to quantify the foraging niche of populations and/or species (Crawford et al. 2008, Yeakel et al. 2016, Giménez et al. 2018, Teixeira et al. 2022). This approach has been used to identify specific dietary items (e.g., krill as dominant prey of North Atlantic fin whales (*Balaenoptera physalus*), (Ryan et al. 2014), monitor changes in diet over time (e.g., Southern right whales (*Eubalaena australis*), van den Berg et al. 2020) and compare foraging niches between baleen whale species (e.g., overlaps of fin, humpback and minke whales in the Antarctic Peninsula, Seyboth et al. 2018). However, due to low population sizes and the logistical challenges of sampling baleen whale tissues in the high seas, few skin biopsy samples are available to assess foraging preferences.

An alternative approach to further our understanding of whale population habits on high-latitude feeding grounds in the Southern Hemisphere is to use historical specimens. Post-mortem, proteinaceous tissues and DNA can preserve for millennia (under appropriate conditions), often making them a reliable time capsule of past populations (Kendall et al. 2018, Raffone et al. 2021). Indeed, historical specimens have been used to infer foraging preferences of animal populations in the current era (Lister & Climate Change Research Group 2011, Schmitt et al. 2018, Palmer et al. 2022), in the past (Alter et al. 2012, Buss et al. 2022) and to estimate changes in foraging preferences over time (e.g., Zenteno et al. 2015, Drago et al. 2017). For example, stable isotope analysis of historical baleen specimens has been used to evidence resource partitioning between fin and sei (*B. borealis*) whales at South Georgia (Buss et al. 2022) and South American fur seals (*Arctocephalus australis*) and sea lions (*Otaria flavescens*) in the western South Atlantic (Drago et al. 2017).

In order to reliably use historical specimens to infer historical foraging preferences, taxonomic information must be accurate. Previously, zooarchaeological assessments were used to infer taxonomy, but whale bones are often highly fragmented and fragmented bones can be inaccurately identified when using zooarchaeological identification methods (Driver et al. 2011, Speller et al. 2016, Moreno-Mayar et al. 2017, van den Hurk 2020, Charpentier et al. 2022). Alternatively, taxonomic information can be determined using DNA-based methods (e.g. Ross et al. 2003, Sremba et al. 2015, 2023, Speller et al. 2016, Seersholm et al. 2021) or Zooarchaeology by Mass Spectrometry (ZooMS), which uses peptide fingerprinting of collagen to identify taxa from archaeological material (Evans et al. 2016, Buckley 2018). Both of these techniques have successfully been used to identify whale bone fragments and improve zooarchaeology identifications (Rastogi et al. 2004, Charpentier et al. 2022).

Here, our study uses DNA and collagen extracted from historical whale bone fragments to accurately assign taxonomy and infer differences in the historical foraging preferences of four baleen whale species in the western South Atlantic using stable isotope analysis. Moreover, we quantify niche specificity and niche overlap of each species, to infer which species are likely to have a restricted diet, and therefore may have the potential to be more vulnerable to the predicted climate change of the 21st century.

2. METHODS

2.1 Research area and samples

Whale bones (*n*=178) were collected in the western South Atlantic (WSA) from beaches located near ex-whaling grounds associated with areas of high numbers of catches of hunted whales during the 20th-century whaling period and are regions known to be whale feeding grounds (Fig. 1, the Falkland Islands, FLK (*n*=58), South Georgia, SG *(n*=89), and the South Orkney Islands, SO (*n*=31); Table S1). Shore-based whaling occurred at the three locations between 1908-1916, 1904-1966, and 1904-1931, respectively (Hart, 2016); the highest quantities of shore-based catches at South Georgia were between the 1910s and 1920s (Hart, 2016). Thus, these bones are likely to represent catches from those periods.

Thirty-four of the Falkland Islands' samples were sampled *in situ* using a handheld drill to obtain ~0.5g of bone shavings (bone surface layers were removed and discarded, drill-bits changed and bleach used between samples). The remaining bone sample fragments were sampled *ex situ* at the British Antarctic Survey (UK) as follows: the outer surface of bone material was removed using a micromotor drill with a 1.8mm diamond ball-shaped rotary burr. Then bone chunks or powder of 0.2 to 0.5g were obtained using a Dremel 3000 with a diamond wheel cutting disc, or a micromotor drill diamond ball-shaped rotary burr, respectively.

2.2 Collagen extractions

Collagen was extracted from bone specimens following (O'Connell et al. 2001**),** but with slight modifications as follows: 0.2 - 0.5g of bone fragments were demineralized at room temperature (~18 - 22°C) following solvent washes of 2:1 chloroform:methanol and 1:2 chloroform:methanol to remove lipids (alternate washes until solution appears colourless). Potential exogenous carbonates were removed from samples using 0.5M aq. hydrochloric acid, until samples softened, and gelatinised at 75°C using acidified deionised water (aq. HCl, pH 3.0). Gelatinised bone collagen was filtered off using Ezee-filters (90um) and the filtrate lyophilised. To identify whether solvent washes altered isotope results, 25 samples were sub-sampled twice and demineralised with and without solvent washes and the isotope results compared using paired t-tests. As no difference was observed in isotope results, but lipid occurrence was visually evident during solvent extraction (milky solution during solvent washes), processing of all subsequent bone samples included a lipid-removal step to prevent lipid-associated biases in δ^{13}C (see Post et al. 2007, Elliott et al. 2017).

2.3 Taxonomic identifications

Taxonomic identifications for 49 of the 178 bone samples were previously published elsewhere (Sremba et al. 2015, 2023). For the remaining 129 samples taxonomic identifications were conducted using DNA and/or peptide profiles as part of this study. For species identification using DNA, extracts were obtained using a modified ancient DNA extraction protocol, as outlined in (Buss et al. 2023) and originally formulated by (Dabney et al. 2013). To summarise, bone powder weighing between 120 and 220 mg per sample was digested in 8M EDTA with Proteinase K (20ug/uL) at 37°C. After 15 minutes the EDTA-Prot K supernatant was removed and replaced (a pre-digestion step) followed by continued digestion of the remaining bone powder at 37°C for 48-72 hours until bone powder was no longer visible to the naked eye. Subsequently, supernatants (1ml) were mixed with binding buffer (13ml) and filtered through High Pure Large Volume Assembly 50 ml (Roche) spin-columns. DNA was eluted in 100µl Tris-Acetate-EDTA (TAE) buffer (2 x 50 µl with an incubation time of 5 minutes at room temperature). All other steps followed (Dabney et al. 2013). Mitochondrial control region sequences were amplified using at least one of three sets of primers targeting fragments of the mitochondrial control region: (1) Dlp5 & Tprowhale; (2) Dlp4 & TProwhale; (3) 337F & Tprowhale; PCR conditions, primer sequences, and genetic sequencing quality criteria are further detailed in Buss et al. (2023) and (Buss 2022). To determine species, mitochondrial control region sequences were compared with known species sequences at NBCI using the Basic Local Alignment Search Tool (BLASTn) and the default parameters (Madden 2003). Unique mitochondrial control region haplotypes of bones collected from the same locality were used to determine whether bone specimens were from different individuals.

Peptide-profiles were used to taxonomically identify 70 of the 178 whale bone samples that were identified using DNA, and to taxonomically identify four samples that failed DNA sequence amplifications. Taxonomic identifications were obtained using peptide fingerprints of re-digested bone collagen (ZooMS) following (Evans et al. 2016). In summary, approximately 0.1mg of bone collagen was suspended in 1000µL of 50mM aqueous ammonium bicarbonate solution (pH 8.0) with 100µL of trypsin enzyme overnight at 37°C in a rocking incubator. The resulting supernatants were acidified with 0.1% aqueous trifluoroacetic acid, purified using 100µL C_{18} resin ZipTip pipette tips (EMD Millipore), washed in conditioning buffer, eluted in 50µL of acetonitrile (50% conc. aqueous solution) and 3µL mixed with α-cyano-4-hydroxycinnamic acid matrix for spotting on a 384-well ground-steel plate in triplicate. Peptide fingerprints were obtained using a calibrated Bruker Ultraflex III matrix-assisted laser desorption/ionization-time of flight (MALDI-TOF) mass spectrometer with a smart beam laser in reflector mode. The resultant spectra were then calibrated and m/z peaks within the data were picked. Identifications were obtained by comparison with published spectra for different species (Buckley et al. 2009, 2014). Taxonomic identifications were assigned at the most conservative level of identification based on the presence of unambiguous m/z markers (peptide spectra used for diagnosability are shown in Table S2). Only bones taxonomically identified to the species-level using DNA and/or peptide-profiles were included in stable isotope analysis. Taxonomic identifications of the 70 samples that underwent both DNA and peptide-profiling were used to check for species identification errors.

2. 4 Stable isotope analysis

Bone collagen extracts were weighed in triplicate for stable isotope analysis (mean ± SD, $\delta^{13}C/\delta^{15}N$: 0.8mg ± 0.1). Carbon and nitrogen isotopic values were measured using a Costech Elemental Analyser coupled in continuous flow mode to a Thermo Delta V Plus continuous-flow stable isotope mass spectrometer (EA-IRMS), at the Godwin Laboratory, University of Cambridge (as in Buss et al. 2022). Measurement precision (δ^{13}C: 0.1‰; δ^{15}N: 0.2‰) was determined using the internationally approved standard (IAEA-600: δ13C=−27.8 ‰, δ15N=1.0 ‰) and in-house standards (nylon: (δ13C=−26.3 ‰, δ15N=−1.6 ‰; alanine: δ13C=−27.4 ‰, δ15N=−1.4 ‰; protein 2 (not specified)). Carbon and nitrogen isotope ratios are expressed as delta values (δ13C and δ15N) relative to international standards (VPDB and AIR, respectively; (Craig 1957, Coplen et al. 2006, Mariotti 1983). Atomic carbon:nitrogen ratios (C:N hereafter) between 3.0 and 3.3 were used to assess sample quality (O'Connell & Hedges 1999, Guiry & Szpak 2020) and triplicate repeats (that passed quality control checks) were averaged prior to statistical analysis.

2.5 Statistical Analysis

Interspecific comparisons of isotopic niches were conducted on four whale species: blue whale (*B. musculus*), fin whale (*B. physalus*), humpback whale (*M. novaeangliae*), and sei whale (*B.borealis*). Due to low sample sizes for the southern right whales (*E. australis*) and sperm whales (*Physeter macrocephalus*), these species were excluded from further comparisons (Table S1 & S3). Differences in stable isotope values within species between sites were assessed using Kruskal-Wallis tests (due to non-normality identified using Shapiro-Wilk normality tests identified in some species (Table S4 & S5)). Intraspecific significant differences between sites were further assessed using post-hoc comparisons with Bonferroni corrections in the R package 'FSA' (DunnTest; Dinno and Dinno 2017). Subsequently, for interspecific comparisons isotope data were pooled across sites assumed to resemble South Atlantic feeding ground demes for species where sites did not significantly differ from one another. As isotopic values differed significantly for humpback whales in the Falkland Islands compared with other sites (Fig. S1), these samples were not pooled with humpback whale data from the two higher-latitude sites (pooled data are presented in Table 1 for info).

Interspecific differences in historical resource use on South Atlantic feeding grounds were determined using bone collagen carbon and nitrogen stable isotope values measured using the R Package SIBER (Jackson et al. 2011b). Historical niche size and percentage overlap in isotopic niche space were assessed using Bayesian estimates of bivariate niche space (SEA_B). In this study, niche size is the multidimensional space defined by stable isotope values (δ^{13}C\\$\delta^{15}$N), reflecting the ecological role, habitat use, and diet of a given species, and serving as a proxy for niche breadth (larger: diet generalists; smaller: diet specialists). Niches were deemed different if 95% credible intervals (95% CIs) of the posterior distributions did not overlap. Graphical representations of isotopic ellipses were drawn using the plotSiberObject function in the R Package SIBER.

The map was produced using qGIS version 3.1 (Quantum 2017) and statistical analyses performed using R version 3.5.2 (R Development Core Team 2003).

Sample ethics statement

All samples involved the use of historical animal tissues obtained post-mortem. Bone collection permits were obtained from the governments of the Falkland Islands and South Georgia and the South Sandwich Islands. All samples were shipped under CITES permits.

3. RESULTS

A total of 174 of the 178 bones were identified as whale; four species of rorqual, blue whale (n=20), fin whale (n=64), humpback whale (n=46), sei whale (n=40) one balaenid (southern right whale) and three odontocetes (all sperm whale) (Fig 1). Mitochondrial control region amplification was successful for 170 bones. Collagen was successfully extracted from 172 of the 174 whale-identified specimens, with 168 overlapping with DNA-identified samples. Four specimens were identified only through peptide fingerprinting, and two had genetic IDs but failed collagen extractions. Of the 172 collagen samples, 155 were of good analytical quality with atomic C:N ratios (between 3 and 3.3), including 151 rorquals (Table S1). Spectra corroborated DNA species identifications and are provided in Table S2. Of the four samples that failed DNA amplification, peptide profiling identified three as carnivorans and one as a cervid–likely pinniped and reindeer (*Rangifer tarandus*), respectively. These are the only known representatives of these groups in South Georgia, with reindeer having been introduced temporarily to provide food for sealers and whalers (Leader-Williams et al. 1989, Burton & Croxall 2012). Although the genetic sequence quality for sample FKB30 was poor, peptide fingerprinting confirmed this sample was a fin whale. Consensus agreements between genetic and peptide fingerprinting were consistent across all samples.

δ^{13}C and δ^{15}N values were available for 19 blue, 57 fin, 37 humpback, and 38 sei whales, respectively, and collectively were not normally distributed (Shapiro-Wilk, $p < 0.05$, Table S4). At the species-level, blue whale and fin whale isotope values were normally distributed, but not sei whale and humpback whale isotope values (Table S4). Therefore, both mean and median δ^{13}C and δ^{15}N values are provided (Table 1). Across all study sites, mean δ^{13}C values (±SD) were as follows: blue whale (-20.5 ± 1.1‰), fin whale (-18.0 ± 1.6‰), humpback whale (-18.9 ± 1.8‰) and sei whale (-13.5 ± 0.8‰). Mean δ^{15}N values (±SD) were: blue whale (6.2 ± 0.8‰), fin whale (7.3 ± 1.0‰), humpback whale (6.9 ± 1.3‰) and sei whale (10.6 ± 1.0‰) (Table 1).

3.1 Intraspecific across-site comparisons

Site-specific bone collagen isotope values are summarised in Table 1 and shown in Fig. 2. For samples with high quality isotope data and mitochondrial control region (n=153), unique mitochondrial control region haplotypes from bones recovered at the same locality were used to assess whether specimens originated from different individuals. Of these, 106 had unique haplotypes. Exclusion of duplicate haplotypes did not affect the overall results (data not shown). Notably, many samples sharing haplotypes also displayed distinct isotope signatures, suggesting they likely originated from different individuals rather than multiple bones from a single adult.

Blue whale samples were available from two sites (SG & SO) and isotopic values did not differ between these sites (Kruskal-Wallis, δ^{13}C: $\chi^2 = 0.32, p = 0.57$; δ^{15}N: $\chi^2 = 0.02, p = 0.90$). In contrast, fin and humpback whales displayed significant site-specific variation ($p < 0.01$ & < 0.005, respectively; Kruskal-Wallis results available in Table S7). Fin whale bones collected in the Falkland Islands exhibited somewhat elevated δ^{13}C and δ^{15}N values compared to those from South Georgia and the South Orkneys (Fig. 3, Table 1), however, post-hoc tests revealed mixed significance among sites (Table S8 & S9). δ^{13}C values in the Falkland Islands were significantly different (+1.5‰) from South Georgia, but not the South Orkneys (Table

S8). Conversely, δ^{15}N values differed significantly between the Falkland Islands and the South Orkneys (+1.0‰), but not South Georgia (Table S9). No significant differences were observed between South Georgia and the South Orkneys for either isotope (Table S8 & S9). Despite these findings, all sites showed substantial overlap in niche size and in bivariate niches even at the 50% level (Fig. S5). Thus, we concluded there are no ecologically meaningful site-specific differences for fin whales, and the observed post-hoc results were likely due to multiple comparisons increasing the change of false positives (type I error). For humpback whales, δ^{13}C and δ^{15}N values were approximately 5‰ and 3‰ higher in Falklands samples relative to South Georgia and the South Orkneys (Fig. 3); sample sizes were small at the Falkland Islands (n = 3) and so should be interpreted with caution. Sei whale isotopic values were primarily derived from Falklands samples (n = 36 of 38), precluding inter-site statistical testing. Results of post-hoc comparison tests are available in Table S8 (δ^{13}C) and Table S9 (δ^{15}N).

3.2 Interspecific within-site comparisons

In the Falkland Islands (no blue whales were identified), δ^{13}C values for sei and humpback whale overlapped (Inter-quartile range (IQR): sei -13.8 to -13.1‰; humpback -14.5 to -13.4‰) (Fig. 2, Table S11). Fin whales had lower δ^{13}C values (IQR: -18.0 to -16.5‰) compared to all other species. Correspondingly, δ^{15}N values were similar between sei whales (IQR: 10.1 to 11.0‰) and humpback whales (IQR: 9.0 to 10.1‰), whilst fin whales had lower values (IQR: 7.7 to 8.4‰) (Fig. 2, Table S12). Additionally, δ^{13}C values for sei and humpback whales were similar to those of two other species collected in the Falkland Islands with small sample sizes: southern right whale (n=1; -15.0‰) and sperm whale (n=3; -13.9 to -13.4‰) (Fig. S1).

At South Georgia (all species), δ^{13}C values differed among species (Table S10). Values were lowest in blue whales (IQR: -21.2 to -19.9‰) followed by humpback whales (-19.8 to -18.8‰), fin whales (-19.2 to -17.7‰) and sei whales (IQR: -15.3 to -13.5‰). In contrast, δ^{15}N values were similar among blue whales (IQR: 5.6 to 7.0‰) and humpback whales (5.7 to 7.7‰) but differed from fin whales (6.6 to 8.0‰) (Table S11). Sei whales showed elevated δ^{15}N values (9.6 to 10.5‰) but could not be statistically compared due to small sample sizes (Table 1, Fig. 2).

At the South Orkneys (no sei whales were identified), δ^{13}C values differed among species (lowest in the blue whale (IQR: -20.7 to -20.0‰) and highest in the fin whale (-19.2 to -17.7‰), with intermediate values for humpback whales (-19.3 to -17.8‰)) (Table S10). In contrast, δ^{15}N values were similar among all three species (blue whales (5.8 to 6.1‰), humpback whales (5.9 to 6.8‰), fin whales (6.3 to 7.1‰)) (Table 1, Fig. 2); pairwise comparisons are in Table S11).

3.3 Ocean-wide interspecific comparisons and isotopic niches

For ocean-basin comparisons, interspecific isotope data that were not significantly different within inter-site post-hoc comparisons were pooled across sites to represent western South Atlantic demes (sites with small sample sizes $n \leq 3$ were excluded). δ^{15}N and δ^{13}C values were significantly different between species (Kruskal-Wallis, δ^{13}C: $\chi^2 = 101.77$, $p < 0.0001$; δ^{15}N: $\chi^2 = 89.893$, $p < 0.0001$). Blue whales (n=19) had the lowest δ^{15}N and δ^{13}C values relative to the other rorqual species, followed by humpback whale (n=34), fin whale (n=57), and sei whale (n=36) (Fig. 4). Post-hoc comparisons showed significant interspecific differences between all species and isotopes except between δ^{15}N of blue whale with humpback whale, and fin whale with humpback whale (Table S12 & S13).

The size of bivariate isotopic niches varied between species (Fig. 4, Table 2). Fin whales had the largest isotopic niche (~4.9) relative to the other three species, suggesting more generalist foraging at the population-level. Humpback whales had an intermediate-sized niche (~3.4) relative to the other species. Antarctic blue whales (~2.7) and sei whales (~2.5) both had smaller isotopic niches, indicative of more specialist foraging strategies at the population-level. Humpback whales from the Falkland Islands were excluded due to small sample sizes (*n*=3), but the unique foraging pattern of the individuals from this site (Fig. 4, Table S5) may indicate increased foraging diversity for humpback whales relative to other rorqual species in the western South Atlantic.

Differences in isotopic niche overlap were observed between species (Fig. 4, Table 3). Sei whales had a distinct isotopic niche that did not overlap with any of the other three species (Fig. 4; Fig. S2, Fig. S3). The isotopic niches of blue, fin and humpback whales all overlapped by varying proportions (Fig. 4). The blue whale niche significantly overlapped with those of humpback whales (Fig. S3 & S4; CI_{50}: 31.6%; CI_{95}: 67.5%) and fin whales (Fig. S3 & S4; CI_{50}: 7.2%; CI_{95}: 63.2%). The isotopic niches of fin and humpback whales also overlapped (Fig. S3 & S4; CI_{50}: 44.3%; CI_{95}: 76.9%).

4. DISCUSSION

Consistent with the competitive exclusion principle, our findings suggest that four baleen whale species partitioned resources across the Southwest Atlantic during the early whaling period (Fig. 4), with blue and sei whales likely being more specialised relative to fin and humpback whales because they occupied smaller isotopic niches. Isotopic niche space has previously been described as an indicator of dietary specialisation (Newsome et al. 2009) with species with increased niche specificity being more vulnerable to environmental change (McKinney 1997, Reynolds 2003). If the smaller isotopic niches of the blue whale and sei whale are consistent with modern-day foraging strategies, these two species may be less adaptable to environmental change. In contrast, the broad isotopic niche of fin whales reflects a more generalist foraging strategy at the population-level, suggesting fin whales may have higher adaptive capacity in the face of climate change relative to blue and sei whales. For humpback whales, we identified two distinct foraging strategies within this breeding population, with humpback whales from the Falkland Islands differing substantially from humpback whales foraging in Southern Ocean waters (Fig S1). This may suggest, like fin whales, that humpback whales are also less susceptible to environmental change through diversification of feeding strategies within the western South Atlantic.

A population of whales that consume multiple prey species with similar isotopic signatures would converge in the same isotopic space, resulting in a narrow isotopic niche. Therefore, narrow isotopic niches do not necessarily indicate dietary specialisation at the population-level (Mathhews & Mazumder, 2004; Yeakel et al. 2016). We argue that this is unlikely to be the case for baleen whales foraging in the Southern Ocean, as multiple studies have demonstrated substantial spatial and temporal variation in the isotopic composition of zooplankton prey in this region (e.g. Seyboth et al. 2018; Stowasser et al. 2012; St John Glew 2021), particularly along latitudinal gradients and with increasing distance from the Antarctic ice edge (Espinasse et al. 2019; Magozzi et al. 2017). Consequently, if whales were feeding on a diversity of zooplankton species or across a range of foraging locations, one would expect broader isotopic niches in this ecosystem. All four rorqual species included in this study are known to consume Antarctic krill to varying degrees (Mackintosh & Wheeler 1929; Brown 1968; Nowacek et al. 2011; Herr et al. 2016), and isotopic values of Antarctic krill themselves have been shown to vary considerably (Stowasser et al. 2012; Zhu et al. 2019). Therefore, the consistently narrow isotopic niches observed for blue and sei whales are more plausibly indicative of dietary specialisation, both at the individual and population levels.

4.1 Feeding specialisations in Falkland Island waters

Except for fin whales, specimens collected from the Falkland Islands regardless of species, exhibited unexpectedly similar bone collagen δ^{13}C values (Fig. 2, Fig. S5). Stable isotope values of proteinaceous tissues are known to systematically reflect foraging locality or environment (Cherel & Hobson 2007, Magozzi et al. 2017, Hobson et al. 2019). Broadly speaking, in marine environments lower baseline δ^{13}C values are observed towards the poles relative to the equator (Magozzi et al. 2017, St John Glew et al. 2021). In contrast, δ^{15}N values, tend to systematically increase with trophic level (Boecklen et al. 2011, Perkins et al. 2014). Owing to variation in baseline marine isoscapes, the δ^{13}C and δ^{15}N values of zooplankton from Falkland Island waters and neighbouring areas on the Patagonian shelf (Troina et al. 2020) are higher on average than δ^{13}C and δ^{15}N values of zooplankton sampled in sub-polar and polar regions; i.e. south of the Subantarctic and polar fronts (Stowasser et al. 2012, Magozzi et al. 2017, Murphy et al. 2021, St John Glew et al. 2021). However, it is important to note that only three humpback whales were sampled in the Falkland Islands, resulting in limited statistical power due to small sample sizes (Table 1). Despite this, the isotope values of these samples did not overlap with or closely align to those of humpback whales from other locations (Fig. 3). Instead, their isotope values were more similar to the values observed in other species sampled in the Falkland Islands (Fig. S5). This pattern suggests the possibility of a unique foraging guild of humpback whales in the western South Atlantic, likely to predominantly feed along the southern Patagonian shelf rather than migrating to Antarctic waters. Such a strategy could enhance population resilience to shifts in prey availability associated with ongoing environmental changes on feeding grounds at higher latitudes. Fin whale specimens collected in the Falkland Islands had higher δ^{13}C and δ^{15}N values (~1.2‰ and ~0.7‰, respectively) compared to those from higher latitudes. However, this difference was relatively small compared to the differences observed in humpback whales (~5.2‰ and ~2.7‰, respectively). Although it is possible that the significant differences observed are due to differences in sample sizes, multiple comparisons and type I error (see 3.1), it is also plausible that the fin whale specimens collected in the Falkland Islands represented a unique group of individuals that forage, at least partially, at the Patagonian shelf, relative to those specimens identified at South Georgia or the South Orkneys. Fin whales are rarely observed in the Falkland Islands to date (Weir, 2022), and historical shore-based whaling operations reported few catches (< 300) in this region (Hart, 2016). Although sightings have increased since the end of commercial whaling (Frans & Augé, 2016), there is currently no evidence of a resident population, and these sightings could represent transient migrants.

Stable isotope analysis of source (e.g. phenylalanine) and trophic (e.g. glutamic acid) amino acids, also referred to as compound-specific isotope analysis, can identify the trophic positioning of consumers and reconstruct the baseline nitrogen isotope value of the system that consumer foraged in (Nielsen et al. 2015; Ishikawa, 2018). To investigate whether fin whales historically foraged in Falkland Islands waters, or the neighbouring Patagonian shelf, future research could apply this approach to compare the isotopic baseline of fin whales specimens recovered in the Falkland Islands with those from other localities, as well as with other species known to forage in the region (e.g. sei whales; southern right whales, Weir 2022).

Humpback whales in the western South Atlantic predominantly represent a single breeding population (commonly referred to as "Breeding Group A" (Fleming & Jackson 2013)). This breeding group is known to have strong site fidelity to feeding grounds near to South Georgia and the South Sandwich Islands (Zerbini et al. 2019, Jackson et al. 2020). Therefore, it was somewhat surprising that the isotopic values of humpback whale bones collected in the Falkland Islands differed from those of South Georgia and the South Orkneys. In the Southern Ocean humpback whales are known to feed on Antarctic krill, alongside other zooplankton species (Nowacek et al. 2011, Bengtson Nash et al. 2018). In contrast, the diet of humpback whales around the Falkland Islands remains undocumented, although recent observations have reported lunge-feeding on shoals of Fuegian sprat, *Sprattus fuegensis* (Weir, pers. comms.). Despite being part of the same breeding population ("Breeding Group G" in the tropical east Pacific: Colombia, Panama and Ecuador), a group of humpback whales from the Southeast Pacific that forage in the Magellan Straits (southern South America) are isotopically distinct from humpback whales that migrate further south to feed (Haro et al. 2021). This demonstrates that humpback whales can display alternative foraging strategies within a single breeding population. Although it would be challenging to increase historical sample sizes due to sampling limitations, humpback whales have been more frequently observed in the Falkland Islands since 2021 (Weir, pers. obs.) and contemporary samples of humpback whales from this region might shed light on whether the unique foraging pattern that we observed persisted into the 21st century.

The majority of the sei whale samples in our study (36 out of 38) were from the Falkland Islands and had the highest δ^{13}C and δ^{15}N values of the four rorqual species (excluding the three humpback whales from the Falkland Islands) (Fig. 4 & S5). This could suggest that they foraged at a higher trophic level and/or at relatively lower latitudes where baseline δ^{13}C values– and to a lesser extent δ^{15}N values– are higher (see Crawford et al. 2008, Hobson et al. 2019). Globally, sei whales primarily forage on low-trophic-level zooplankton, such as euphausiids, decapod larvae, copepods, and small forage fishes (Mackintosh 1946, Brown 1968, Horwood 1987, Flinn et al. 2002, Silva et al. 2019, Reiss et al. 2020, Takahashi et al. 2022), suggesting that their higher δ13C and δ15N values are unlikely to be linked to higher trophic-level foraging. The distinct isotopic niche of sei whales in our study may indicate that they historically foraged near the Falkland Islands and southern Patagonian waters and were less likely to feed in Southern Ocean waters, as seen in the isotopic niches of other rorqual species (Fig. 4). Differences in the feeding areas of sei whales may also be supported by historical stomach contents data (Matthews 1938). Empty or near empty stomachs were reported in the vast majority of sei whales captured around South Georgia between 1927- 1931 by the Discovery Expedition, contrasting with other large rorqual species. While this was originally interpreted as a reflection of krill shortages (Matthews 1938), it is possible that the data reflect historical differences in sei whale feeding grounds compared with those of other rorquals.

The Falkland Islands remains a known foraging ground for contemporary sei whales (Baines & Weir 2020, Weir et al. 2021), suggesting this region has been a key foraging area for 5-6 generations (given the generation time of a sei whale is 23.3 years, Taylor et al. 2007). The narrow isotopic niche and consistent foraging patterns imply that sei whales in the western South Atlantic may be diet specialists, potentially making them less adaptable to 21st-century climate changes. This finding was unexpected, as sei whales are generally regarded as diet generalists known to use diverse foraging strategies (i.e lunge or skim feeding) to exploit prey patches of varying densities and species in other regions (Horwood 1987). Further research on their foraging preferences near the Falkland Islands is needed to determine whether their diet remains specialised to date.

Isotopic ratios of collagen extracted from adult mammalian bone reflect an individual's average diet over many years (likely >7 years in larger mammals, but precise turnover rates are unknown for baleen whales, and rates are likely to vary by bone type and animal age) (Hobson & Clark 1992, Hedges et al. 2007, Newsome et al. 2010, Matsubayashi & Tayasu 2019, Taguchi & Lopez 2021). The higher $\delta^{13}C$ values measured in all whale bones collected in the Falkland Islands, regardless of species (Fig 2 & S5), suggest that this region likely served as a significant feeding ground for many species, rather than a temporary stopover on the way to higher latitudes. If the bones had come from individuals that fed south of the Subantarctic and polar fronts and simply passed by or stopped over near the Falkland Islands on their journeys to wintering sites at lower latitudes, their $\delta^{13}C$ values would be more similar to those found at South Georgia and the South Orkneys (comparable results can be found in this study alongside previous studies (Seyboth et al. 2018, Buss et al. 2022)). The suggestion that the Falkland Islands may have been an important feeding ground for many whale species is perhaps unsurprising given that the oceanographic dynamics of the marine habitats surrounding the Falkland Islands are characterised by high primary productivity associated with the mixing of temperate and Subantarctic water masses (van der Grient et al. 2023). The great whales foraging in the Falkland Islands may represent a unique predator guild subject to different environmental pressures relative to other rorqual species that migrate to Antarctic waters to feed.

4.2 Feeding specialisations in the Southern Ocean

The majority of humpback whales (43 of 46) identified in our study were from South Georgia and the South Orkneys, two known humpback whale feeding grounds in the Southern Ocean (Orgeira et al. 2017, Zerbini et al. 2019, Bamford et al. 2022). As mentioned above, humpback whales in the western South Atlantic mostly belong to "Breeding Group A" (Fleming & Jackson 2013); a group of individuals known to have strong site fidelity to feeding grounds near to South Georgia and the South Sandwich Islands (Zerbini et al. 2019, Jackson et al. 2020). Therefore, it was unsurprising that the isotope values of humpback whales identified at South Georgia were similar to one another (Fig. 3) and consistent with feeding on Antarctic krill (alongside other low-trophic-level prey at sub-polar latitudes) (Stowasser et al. 2012, Seyboth et al. 2018, Zhu et al. 2019). Humpback whale diets at the South Orkneys has not been characterised previously, but the similar isotope values that we observed between samples collected in the South Orkneys and South Georgia suggests similar feeding strategies. The genetic identities of humpback whales from the South Orkneys were previously thought to belong to Breeding Group G in the eastern South Pacific (Dalla Rosa et al. 2012), however more recent findings suggest it is likely to be a mixture of individuals from both the Atlantic and Pacific (Marcondes et al. 2021). Either way, the similarities of $\delta^{13}C$ and $\delta^{15}N$ values of all individuals from this region suggest similar feeding strategies, regardless of breeding population.

All humpback whales from South Georgia and the South Orkneys contrasted substantially from the three humpback whales from the Falkland Islands, which had much higher $\delta^{13}C$ values consistent with zooplankton predators that forage in Falkland Island shelf waters today (Humpback whale $\delta^{13}C$ range: -16.8 to -14.5‰ (assuming a Suess correction of 1.19‰ between 1916 (when shore-based whaling ceased in the Falkland Islands) and contemporary studies); dolphin gull, *Leucophaeus scoresbii*: -16.5‰ to -18.0‰; (Masello et al. 2013); multiple marine predators: -15.0 to -18.0‰ (Weiss et al. 2009); see (Eide et al. 2017, Williams et al. 2021) (and references within) for details on the Suess effect). The high proportion of humpback whale individuals with foraging strategies indicative of Antarctic krill, supports previous research suggesting Antarctic krill and Antarctic and sub-Antarctic waters are an essential part to the life histories of humpback whales from Breeding Group A in the western South Atlantic, and potentially Breeding Group G in the South Pacific. Future work understanding the genetic identity of humpback whales at the South Orkneys could build upon previous research understanding gene flow and connectivity between these two regions (e.g. Cypriano-Souza et al. 2017, Sremba et al. 2023).

Antarctic blue whales are krill specialists and Antarctic krill has been an abundant food supply in this region for centuries (S. 1962, Goodall-Copestake 2010). In our study, blue whales had the lowest $\delta^{13}C$ and $\delta^{15}N$ values and a constrained isotopic niche consistent with feeding on Antarctic krill, *Euphausia superba* (Mackintosh & Wheeler 1929, Kawamura 1980). The historical niche of Antarctic blue whales that we observed here is similar to that previously observed for contemporary Antarctic blue whales at the Antarctic Peninsula (Seyboth et al. 2018). Our findings suggest that the specialised foraging strategy of Antarctic blue whales has been consistent for at least a century. Climatic changes to Southern Ocean ecosystems are ongoing (Whitehouse et al. 2008, Flores et al. 2012, Trathan et al. 2012, McBride et al. 2021), including spatiotemporal changes in Antarctic krill availability (Atkinson et al. 2019). Our findings suggest that the Antarctic blue whale may have less adaptive capacity to adjust foraging strategies relative to other sympatric baleen whale species, including fin whale and humpback whale. Although Antarctic blue whale numbers appear to be increasing in some parts of the South Atlantic (Calderan et al. 2020), their population size is still small (< 4000 individuals (Olson et al. 2024) and the restricted isotopic niche is a cause for concern under climate change, especially given that genetic diversity declines have also been observed for this species in the South Atlantic since the cessation of commercial whaling (Sremba et al. 2023); both low genetic diversity and dietary specialism are characters of extinction vulnerability (Dulvy et al. 2003, Frankham 2005, Petchey et al. 2008, Richards et al. 2021). At the same time, a growing commercial krill industry is targeting the food supply for Antarctic blue whales and increasing the potential for fishery-whale conflict (Trathan 2023a b), with potential fatalities (Ryan et al. 2023). This could result in reduced prey availability for recovering Antarctic blue whale populations. Therefore, the consistent dietary specialism of Antarctic blue whales should thus be considered when planning for effective conservation management under climate change.

The niche breadth of fin whales in our study is consistent with broad isotopic niches exhibited by other marine predators (Dehnhard et al. 2020, Walters et al. 2020, van den Berg et al. 2020, Ciancio et al. 2021). $\delta^{13}C$ values suggest fin whales are targeting a large range of carbon sources (probably across a wide range of latitudes), providing support for fin whales having increased adaptive capacity in the face of environmental change relative to other whale species. Our findings support previous findings that showed a wide range of $\delta^{13}C$ values in fin whales by measuring stable isotope ratios of baleen plates from five individuals from the 1940s (Smith et al. 2024). Fin whales are known to forage on Antarctic krill (Mackintosh & Wheeler 1929, Mackintosh 1946, Ryan et al. 2023) and *Thysanoessa macrura* (Herr et al. 2016), but the large dietary breadth we observed suggests that they may also forage on other taxa. Unlike the Antarctic blue whale, the genetic diversity of fin whales is much higher, indicative of a large, or old, effective breeding population and that high mitochondrial genetic diversity has been retained since whaling (Buss et al. 2023, Sremba et al. 2023). Their generalist foraging strategy and high genetic diversity may be contributing factors as to why fin whales have recovered substantially despite being the most heavily hunted species in terms of absolute abundance during the 20th century (> 700,000 Southern Hemisphere fin whales (Rocha et al. 2015)).

Southern Hemisphere baleen whales are recovering from centuries of exploitation (Zerbini et al. 2019, Jackson et al. 2020, Calderan et al. 2020) during a period of anthropogenic and environmental change (Flores et al. 2012, Turvey & Crees 2019, Duarte et al. 2021, Kabir et al. 2023). Although there is some concern that the return of whales to Southern Hemisphere ecosystems may result in increased competition with other marine predators (Surma et al. 2014, Hofman 2017, Reisinger et al. 2022, Savoca et al. 2024), it is likely that the return of whales will result in increased trophic coherence and improved food web stability (see (Johnson et al. 2014)). Whale defecation is known to increase the translocation of nutrients through the water column and has been linked to increases in primary productivity (Roman & McCarthy 2010, Roman et al. 2014). As whales return it is plausible that this may facilitate increases in plankton biomass and foster oceanic carbon sequestration.

4.3 Future considerations

Our study showed that at least four rorqual species partitioned resources consistent with the Competitive Exclusion Principle (Fig. 4). It is likely that at least one of these species, the sei whale, had an isotopic niche vastly different from those of the other three species likely due to foraging in non-polar waters (Falkland Islands) (Weir et al. 2019, Buss 2022). However, limited information is available to determine what the drivers were for resource partitioning (inferred through low rates of overlap in isotopic niches) between blue, fin, and humpback whales at South Georgia and the South Orkney feeding grounds, especially given all three species have been reported feeding on Antarctic krill (*E.superba*) at these regions (Nowacek et al. 2011, Herr et al. 2016, Miller et al. 2019). There is some indication that fin and humpback whales partition Antarctic krill by foraging at varied depths (Herr et al. 2016) and varied krill size-selectivity (Santora et al. 2014). Blue and fin whales may forage at different latitudes, with the former more polar and the latter more sub-polar (Mackintosh & Wheeler 1929). Blue and humpback whales have been observed foraging in close proximity on Antarctic krill, with Antarctic blue whales observed feeding on shallow, high-density swarms (Miller et al. 2019), and hypothesised to be more depth-limited in their foraging due to their larger size (Goldbogen et al. 2012). Although these three species are known to feed on Antarctic krill, with size-selectivity differences observed between species (Friedlaender et al. 2021, Cade et al. 2022, Goldbogen et al. 2023), there is a wide variety of zooplankton and krill species in sub-Antarctic and Antarctic waters (Stowasser et al. 2012, Pinkerton et al. 2020). The niche variation hypothesis proposes that species characterised by utilising a broad range of resources are, in fact, composed of heterogenous groups of relatively specialised individuals (Bolnick et al. 2007). This has been shown to be true using stable isotopes in both marine (e.g. loggerhead turtles, Vander Zanden et al. 2010) and terrestrial species (e.g. stoats, McAulay et al. 2021). Thus, it is plausible that some of the intraspecific isotopic variation observed in baleen whales in our study reflects differences in prey choice. We detected a wide range of resource use in fin whales, but not in the other species. Fin whales are known to forage predominantly on *Euphausia sp.,* alongside other zooplankton to a lesser extent (Mackintosh and Wheeler 1929, Herr et al. 2016). Therefore, we hypothesis that the inter-individual variation observed is more likely driven by spatial variation in foraging behaviour, rather than by differences in prey selection. Indeed, previous research has shown that some fin whales forage during migration, while others do not forage when not on high latitude feeding grounds, or perhaps remain in the Southern Ocean year-round–both scenarios would result in similar isotope signatures (see Buss et al. 2022). A better understanding of prey choice on the feeding grounds, alongside comprehension of the proportion of the diet consumed during migration, is essential to fully understand intraspecific and interspecific food-web dynamics and to implement effective management plans as whales recover.

Our study demonstrates that historical isotopic niches can provide valuable insights into the foraging breadth and potential vulnerabilities of recovering baleen whale populations, which are often challenging to observe and sample in the high seas. The use of stable isotopes and isotopic niche size estimation from historical specimens represents a cost-effective and accessible approach to reconstructing past foraging preferences, offering a robust framework for assessing diet specialisation and extinction vulnerability. Although commonly applied to terrestrial species (e.g. Cheeseman et al. 2021, Fox et al. 2023), this method has significant potential for broader applications to marine megafaunal populations, especially those with highly-migratory predominantly offshore distributions. Future studies should take advantage of the extensive natural history collections that exist (Benham & Bowie 2022) as the integration of isotopic niche estimation and temporally resolved datasets could be more widely used as a cost-effective, and accessible palaeoecological indicator for diet specialism and extinction vulnerability for marine megafaunal populations worldwide.

5. CONCLUSION

Stable isotope analysis of historical whale bones suggest that the coexistence of baleen whales on summer feeding grounds in the past was facilitated by resource partitioning, when whale populations were close to carrying capacity. As whale populations recover and competition for food increases, it might be expected that similar niche partitioning will recur and/or increase, which could result in increased food-web stability. Here, we identified that the historical isotopic niches differed in size between species. At the population-level, blue whales were dietary specialists and sei whales were dietary specialists, likely foraging predominantly in polar and Patagonian shelf waters, respectively. The isotopic niche of fin whales suggests that they were dietary generalists with humpback whales' diets being more intermediate, likely foraging predominantly in polar and sub-polar habitats. Our results suggest that a unique foraging group of humpback whales may have existed in the Falkland Islands during the whaling period and further research is required to explore whether this is still the case. These data provide a baseline to assess the foraging niches and infer the ecological implications of recovering migratory whale populations in the western South Atlantic. This information is vital given the likely changes in ocean productivity and circulation that are predicted during this century owing to climate change.

6. DATA AVAILABILITY

Stable isotope values ($\delta^{13}C$, $\delta^{15}N$), C:N ratios and metadata of historic bone collagen samples can be downloaded from the British Antarctic Survey Polar Data Centre titled: *"Stable isotope values ($\delta^{13}C$, $\delta^{15}N$) and C:N ratios of bone collagen samples for six whale species, Antarctic blue whale (Balaenoptera musculus intermedia), fin whale (Balaenoptera physalus), humpback whale (Megaptera novaeangliae), sei whale (Balaenoptera borealis), southern right whale (Eubalaena australis), and sperm whale (Physeter macrocephalus). Bone samples were collected from ex-whaling sites across three locations in the western South Atlantic: the Falkland Islands, South Georgia, and the South Orkneys."*

7. ACKNOWLEDGEMENTS

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FIGURES

Figure 1. A) Map of the South Atlantic Ocean showing the locations of the three island archipelagos where whale bones were collected. Sites are marked with arrows as follows: FLK = Falkland Islands; SG = South Georgia; SO = South Orkneys. B) Proportional composition of identified Cetacea from bone assemblages pooled across all sites (left), and at each site (FLK, SG, SO). Species were identified using peptide fingerprinting and/or Sanger-sequencing of the mitochondrial control region. Percentages and counts of each species are overlaid on bar charts.

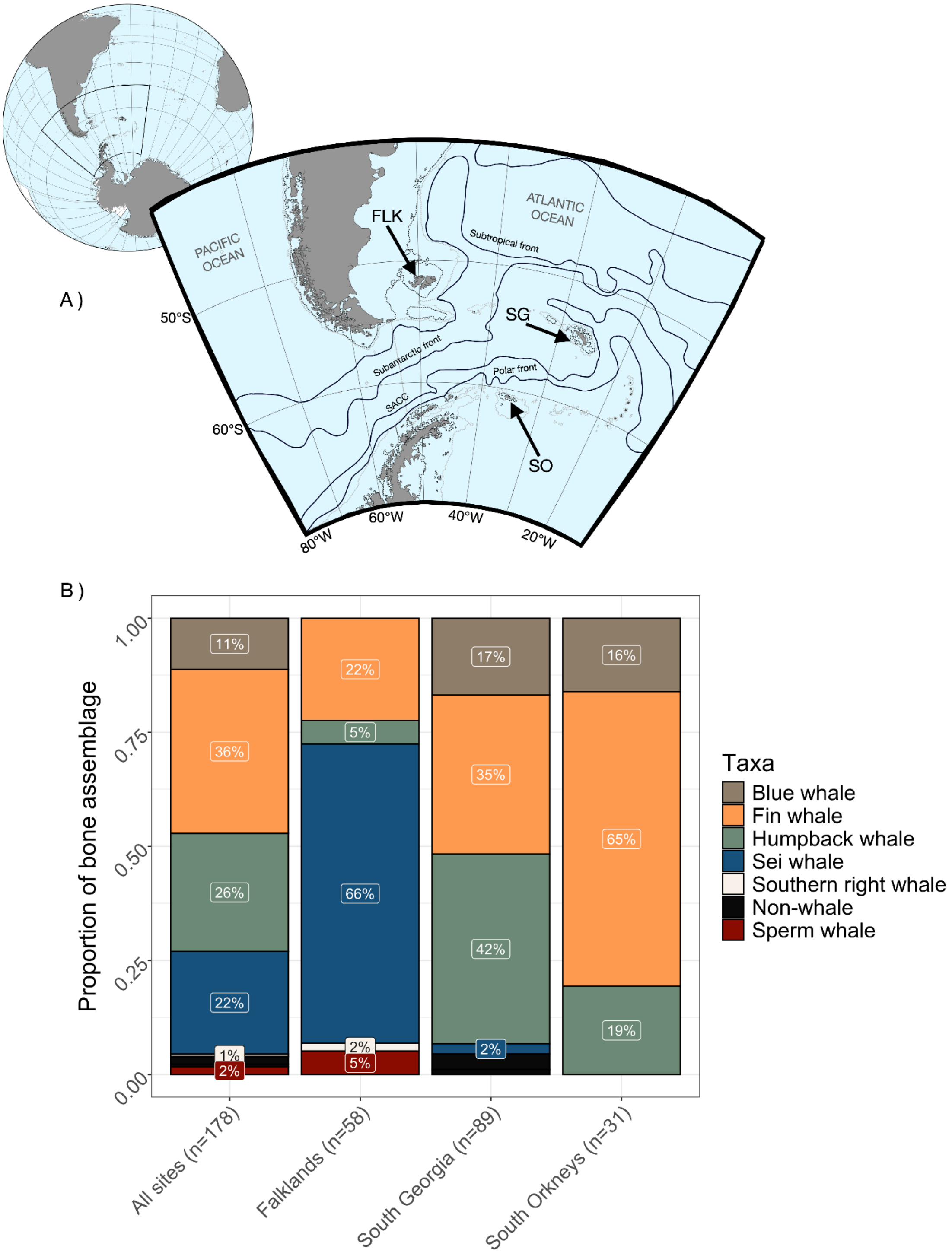


Figure 2. Stable isotope values (δ^{13}C and δ^{15}N) of whale bone collagen from six whale species collected across three sites: Falkland Islands (FLK), South Georgia (SG), and the South Orkneys (SO). A) δ13C values and B) δ15N values of bone collagen, showing variations across species and locations. Box plots display the interquartile range (IQR; 25th–75th percentiles), with whiskers extending to 1.5 x 1QR. Data points outside this range are plotted individually as outliers. Red circles denote group means.

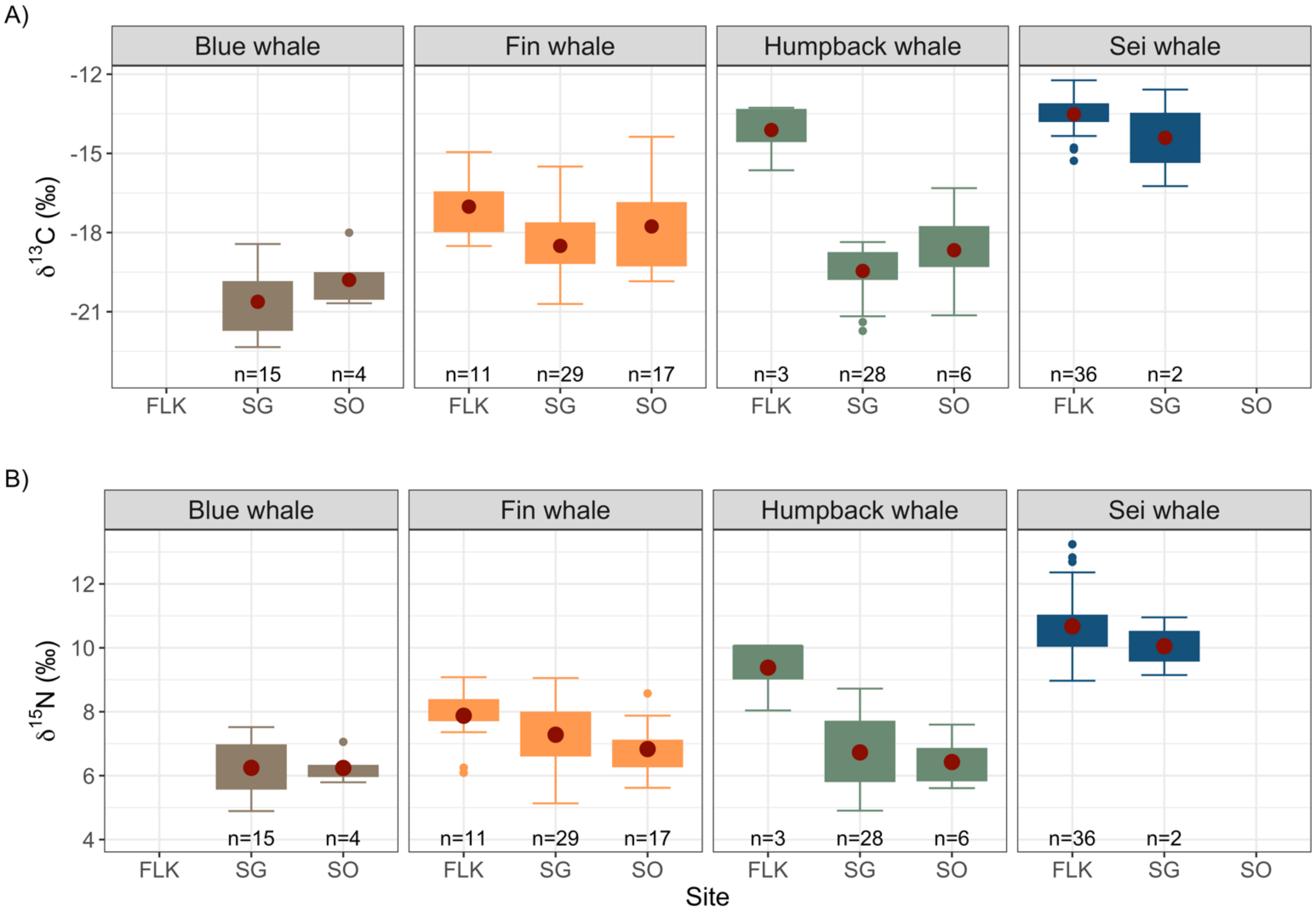


Figure 3. Stable isotope values (A) δ13C and B) δ15N) of whale bones from fin and humpback whale species collected across three sites: Falkland Islands (FLK), South Georgia (SG), and South Orkneys (SO). FLK humpback whales are relatively enriched compared to humpback whales from other sites and from FLK fin whales. Pairwise statistical significance from post-hoc comparisons are shown (see S14 & S15) as follows: *p* < 0.001 = **; *p* < 0.05 = *; Not significant = NS.

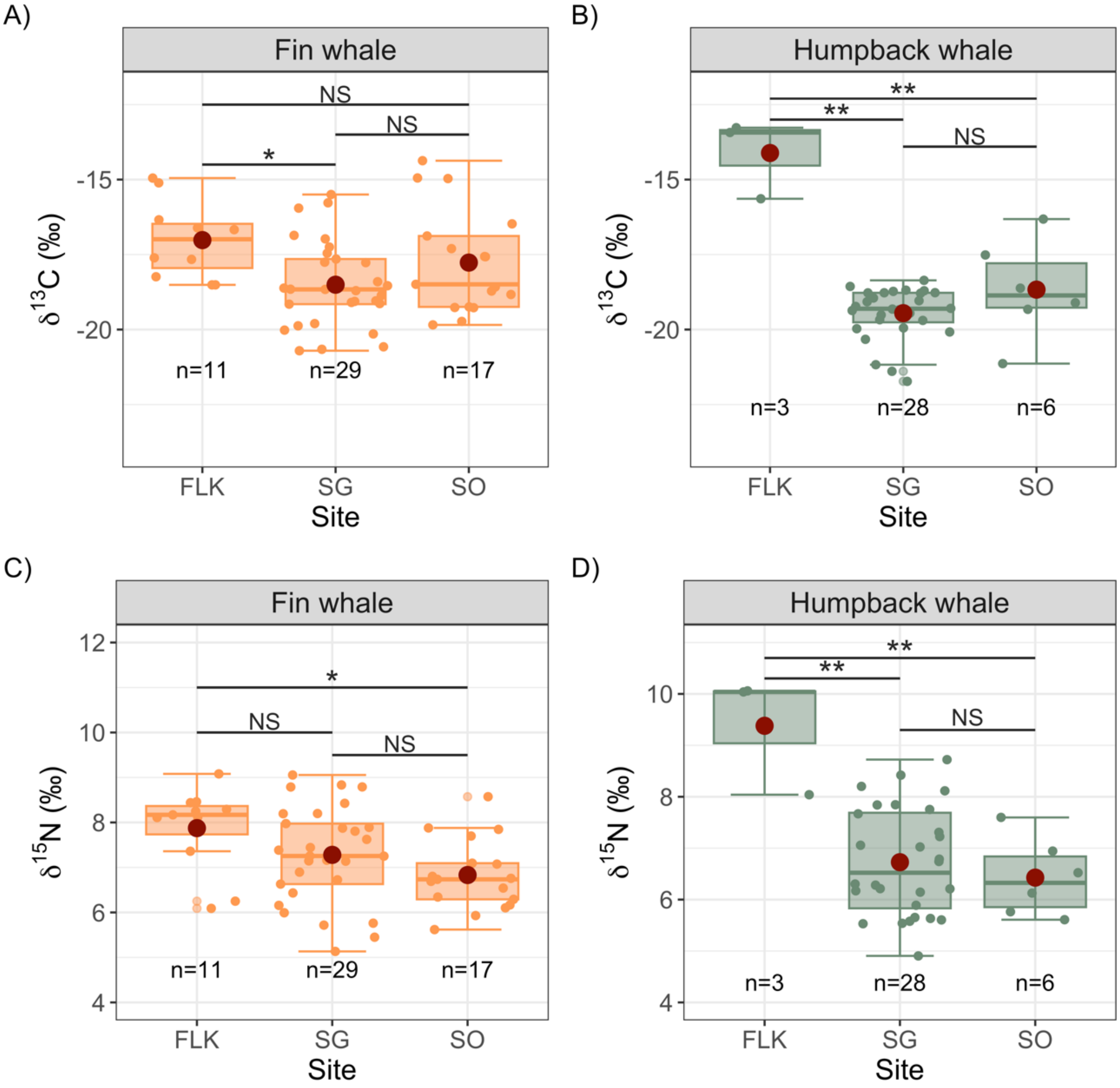
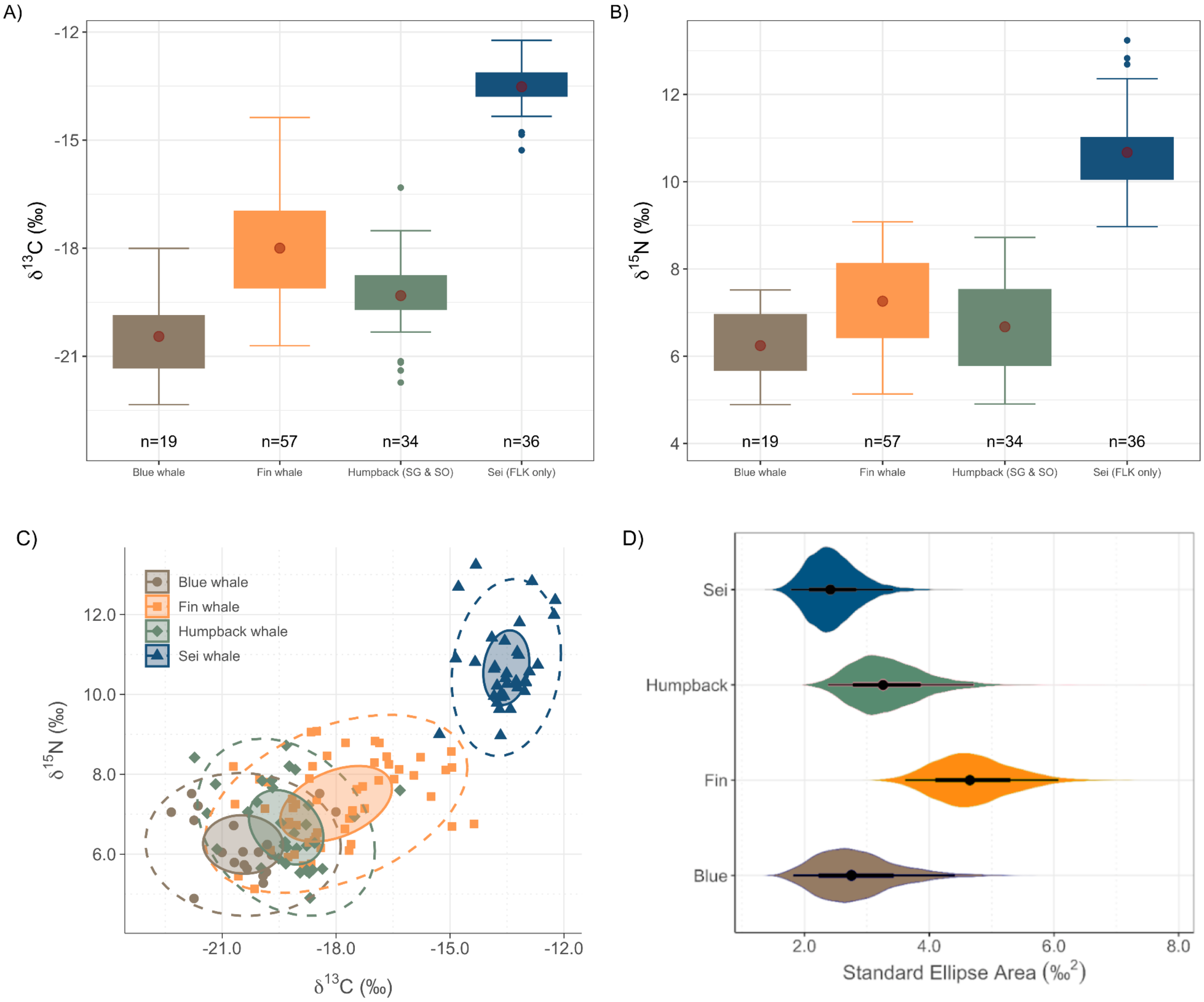


Figure 4. Stable isotope values of collagen extracted from whale bones collected across the western South Atlantic:: A) δ13C values; B) δ15N values; C) Variation in bivariate isotopic niches (δ13C & δ15N values) highlighting variations in foraging niches between species, with 50% (inner contour, solid line) and 95% (outer contour, dotted line) bivariate normal ellipses, displaying the core and total isotopic niches; D) Bayesian stable isotope ellipse areas (*SEAb*) from SIBER analysis (Jackson et al. 2011a). Higher and lower values are indicative of more generalist or specialist population-level foraging, respectively. Box plots with IQR. Group means shown as red circles.



TABLES

Table 1. Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope values of whale bone collagen for six cetacean species collected from three sites in the South Atlantic. All included samples had an atomic C:N ratio between 3.0 and 3.3.

Species	Site	*n*	δ^{13}C (median + IQR)	δ^{15}N (median + IQR)	δ^{13}C (mean +SD)	δ^{15}N (mean +SD)
Blue whale	All	19	-20.4 (-21.2, -19.9)	6.24 (5.6, 6.9)	-20.5 (1.1)	6.2 (0.8)
	SG	15	-20.4 (-21.7, -19.9)	6.0 (5.6, 7.0)	-20.6 (1.1)	6.2 (0.8)
	SO	4	-20.5 (-20.7, -20.0)	6.1 (5.8, 6.1)	-20.0 (1.2)	6.1 (0.6)
Fin whale	All	57	-18.0 (-19.1, -17.0)	7.3 (6.4, 8.1)	-18.0 (1.6)	7.3 (1.0)
	FLK	11	-17.0 (-18.0, -16.5)	8.2 (7.7, 8.4)	-17.0 (1.2)	7.9 (0.9)
	SG	29	-18.7 (-19.2, -17.7)	7.3 (6.6, 8.0)	-18.5 (1.4)	7.3 (1.1)
	SO	17	-18.5 (-19.2, -16.9)	6.7 (6.3, 7.1)	-17.8 (1.7)	6.8 (0.8)
Humpback whale	All	37	-19.2 (-19.7, -18.7)	6.6 (5.8, 7.7)	-18.9 (1.8)	6.9 (1.3)
	FLK	3	-13.4 (-14.5, -13.4)	10.0 (9.0, 10.1)	-14.1 (1.3)	9.4 (1.2)
	SG	28	-19.3 (-19.8, 18.8)	6.3 (5.7, 7.7)	-19.5 (0.8)	6.7 (1.1)
	SO	6	-18.9 (-19.3, -17.8)	6.3 (5.9, 6.8)	-18.7 (1.6)	6.4 (0.8)
Sei whale	All	38	-13.5 (-13.8, -13.1)	10.4 (10.0, 11.0)	-13.5 (0.8)	10.6 (1.0)
	FLK	36	-13.5 (-13.8, -13.1)	10.4 (10.1, 11.0)	-13.5 (0.7)	10.7 (1.0)
	SG	2	-14.4 (-15.3, -13.5)	10.1 (9.6, 10.5)	-14.4 (2.6)	10.1 (1.3)

Table 2. Isotopic niche size (SEAb) based on mean $\delta^{13}C$ and $\delta^{15}N$ values of historic bone collagen from four whale species in the South Atlantic. Niche sizes were estimated using the R Package SIBER (Stable Isotope Bayesian Ellipses) (Jackson et al. 2011b). The analysis includes samples aggregated from three bone collection sites: Falkland Islands (FLK), South Georgia (SG), and South Orkneys (SO). Niche size estimates are provided for blue, fin, and sei whales, with 95% credible intervals for each species' isotopic niche size shown in parentheses. Previously presented mean $\delta^{13}C$ and $\delta^{15}N$ values are shown alongside for reference.

Species	***n***	**Niche size (SEAb)**	**$\delta^{13}C$ (mean +SD)**	**$\delta^{15}N$ (mean +SD)**
Blue whale	19	2.7 (1.7 - 4.0)	-20.5 (1.1)	6.2 (0.8)
Fin whale	57	4.9 (3.6 - 6.2)	-18.0 (1.6)	7.3 (1.0)
Humpback whale$_{\text{(SG \& SO only)}}$	34	3.4 (2.5 - 4.5)	-19.3 (1.0)	6.6 (1.0)
Sei whale	36	2.5 (1.88 - 3.3)	-13.6 (0.8)	10.6 (1.0)

Table 3. Interspecific overlap in isotopic niches based on Stable Isotope Bayesian Ellipses (SIBER) analysis. The 50% isospace overlap is represented above the diagonal, while the 95% isospace overlap is shown below the diagonal. The range of overlap values, calculated from random sub-sampling of the data, is provided in parentheses to indicate the variability in niche overlap across different sub-samples. This analysis offers insights into the degree of resource partitioning and dietary niche overlap between species.

	Blue whale	**Fin whale**	**Humpback whale**	**Sei whale**
Blue whale		7.2 (0.0 - 28.9)	31.6 (0.0 - 76.2)	0.0 (0.0 - 0.0)
Fin whale	63.2 (34.8 - 91.9)		44.3 (10.8 - 74.6)	0.0 (0.0 - 0.0)
Humpback	67.5 (42.2 - 88.8)	76.9 (51.4 - 95.1)		0.0 (0.0 - 0.0)
Sei whale	0.0 (0.0 - 0.0)	0.1 (0.0 - 29.3)	0.0 (0.0 - 0.0)	

For supplementary data please see separate document.

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