



Evidence of resource partitioning between fin and sei whales during the twentieth-century whaling period

Danielle L. Buss^{1,2} · Ella Hearne³ · Rebecca H. Y. Loy³ · Andrea Manica³ · Tamsin C. O'Connell² · Jennifer A. Jackson¹

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Abstract

Investigating resource partitioning of marine predators is essential for understanding coexistence of sympatric species and the functional role they play in marine ecosystems. Baleen whales are a key component of sub-Antarctic ecosystems, foraging predominantly on zooplankton and small forage fish. During the twentieth century, baleen whales were unsustainably exploited across the Southern Ocean. Within the exclusive economic zone of South Georgia and the South Sandwich Islands (SGSSI EEZ) in the South Atlantic, approximately 98,000 fin whales (*Balaenoptera physalus*) and 16,000 sei whales (*B. borealis*) were harvested. Despite both species historically occurring in high numbers and feeding in sub-polar waters, little is known about the mechanisms of coexistence. Here, by measuring stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in archived baleen plates and analysing historic catch data, we investigate resource partitioning of fin and sei whale during the commercial whaling period. Temporal and spatial occupancy at SGSSI EEZ (inferred from whaling catches that occurred between 1904 and 1976), alongside historic stomach contents (from the literature), and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ results (observed in this study), suggests that despite using a common prey resource there was limited overlap in isotopic niches between the two species, with sei whales using SGSSI waters later in the season and for a shorter period than fin whales. We hypothesise that the isotopic differences were most likely due to sei whales foraging at lower latitudes prior to arrival at SGSSI. Our data provide novel insight into how two sympatric whale species co-occurring at SGSSI during the commercial whaling period may have partitioned resources and provide a potential ecological baseline to assess changes in resource use in recovering whale populations.

Keywords *Balaenoptera borealis* · *Balaenoptera physalus* · Resource partitioning · Stable isotope analysis · Whaling; South Georgia · Baleen

Introduction

Resource partitioning is a mechanism that facilitates the coexistence of sympatric species within an ecosystem (Levin 2000; Roques and Chekroun 2011; Friedlaender et al. 2021). This mechanism, commonly referred to as the competitive exclusion principle, states that two species cannot occupy exactly the same niche and stably coexist (Hardin 1960), with “niche” previously defined as the ecological space where a species or population can persist and thus utilise resources and impact its environment (Polechová and Storch 2019) (although other similar definitions exist e.g. Grinnell 1924; Leibold 1995). Instead, to reduce competition sympatric species may target different prey taxa, different size classes of the same prey taxa, or target the same prey taxa at different times of day (or year), in different locations, or both

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✉ Danielle L. Buss
daniellebuss277@gmail.com

¹ British Antarctic Survey, National Environment Research Council, Cambridge CB3 0ET, UK

² Department of Archaeology, University of Cambridge, Downing Street, Cambridge CB2 3DZ, UK

³ Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

(spatiotemporal partitioning) (Garneau et al. 2007; Gerrish and Morin 2016; Fossette et al. 2017; Morera-Pujol et al. 2018; Gulka et al. 2019; Lea et al. 2020; Teixeira et al. 2021; Durante et al. 2021; Friedlaender et al. 2021). For example, whale species foraging on Antarctic krill near the Antarctic Peninsula between summer and autumn appear to differentiate krill prey by size class with humpback, Antarctic minke, and fin whales targeting small (< 35 mm), intermediate (35–44 mm), and large (> 45 mm) krill, respectively (Santora et al. 2010). In contrast, bull sharks and Atlantic tarpon in the tropical North Atlantic target the same prey groups within the same region at different times of the year (Hammerschlag et al. 2012), whilst blue and fin whales in the eastern North Pacific forage on similar prey over the same time period at different depths (Friedlaender et al. 2015). Ecosystem-based management can only be implemented effectively once the mechanisms facilitating resource partitioning and coexistence of marine predators on feeding grounds are known (e.g. fisheries closures coordinating with marine mammal occurrence and life history strategies to prevent accidental bycatch O’Keefe et al. 2013; Hoos et al. 2019)).

Understanding resource partitioning of Mysticeti (baleen whales) is important as they are top marine predators that provide essential ecosystem services, including the transfer of nutrients between the many habitats and regions of which they occur (Roman et al. 2014; Doughty et al. 2016). Moreover, engulfment foraging combined with large body size gives baleen whales the capacity to disproportionately impact ecosystem functioning relative to other top marine predators (Doughty et al. 2016; Goldbogen et al. 2017). Due to their large energetic requirements, baleen whales are often associated with highly productive areas of the ocean where they can target dense aggregations of prey (Kelt and Van Vuren 1999; Goldbogen et al. 2017; Kahane-Rappaport et al. 2020; Cade et al. 2021a, b). These ephemeral prey hotspots (densely packed high-quality and often sporadic prey swarms) often facilitate resource competition by enticing multiple species and large numbers of baleen whales to forage in close proximity (Findlay et al. 2017; Cade 2021a; Rockwood et al. 2020; Cade et al. 2021b). However, the mechanisms driving the coexistence of mixed species aggregations of baleen whales are relatively understudied compared with other taxonomic groups, including but not exclusive to, seabirds (Robertson et al. 2014; Navarro et al. 2015; Pontón-Cevallos et al. 2017; Gulka et al. 2019; Reisinger et al. 2020; Mills et al. 2021) and marine fishes (Targett 1978; Ross 1986; Fanelli et al. 2011; Cherel et al. 2011; Lopez-Lopez et al. 2011; Sheaves et al. 2013; Pardo et al. 2015; Drago et al. 2017). Recent publications have demonstrated resource partitioning amongst baleen whales (McCarthy et al. 2021; García-Vernet et al. 2021). Baleen whale species have been observed foraging

in common areas at different trophic levels (Gavrilchuk et al. 2014; Witteveen and Wynne 2016; Herr et al. 2016), whilst, at one well-documented feeding site, different species partition the same prey taxa by size class, depth, and distance to shore (Friedlaender et al. 2009, 2021). It is evident that whales can use a variety of mechanisms to facilitate sympatry; understanding these is important to identify foodweb dependencies and develop effective ecosystem-based management.

In the Southern Hemisphere, multiple species of baleen whales migrate to highly productive Antarctic and sub-Antarctic waters during the austral summer to feed (Mackintosh and Wheeler 1929; Mackintosh 1946; Nemoto 1962; Kawamura 1980), facilitating the potential for resource partitioning. The high latitudes of the South Atlantic represent some of the most productive and biodiverse areas in the Southern Ocean (Atkinson et al. 2001; Trathan et al. 2007, 2014) and baleen whales form a key component of marine predator guilds here (Brown 1968; Headland 1992; Zerbini et al. 2006; Kennedy et al. 2020). Marine resources around South Georgia and the South Sandwich Islands (SGSSI) in the South Atlantic are monitored and managed by the government of SGSSI within the boundaries of the SGSSI exclusive economic zone (EEZ). Since twentieth-century whaling ceased in 1986 (Rocha et al. 2015), there is now evidence of whale population size increases at SGSSI (Kennedy et al. 2020; Jackson et al. 2020; Baines et al. 2021). Of the five species that currently forage at SGSSI, or were observed foraging at SGSSI during the twentieth-century whaling period (blue whale, *Balaenoptera musculus*, fin whale, *Balaenoptera physalus*, humpback whale, *Megaptera novaeangliae*, Antarctic minke whale, *Balaenoptera bonaerensis* and sei whale, *Balaenoptera borealis*), two species (fin and sei whale) occurred sympatrically in sub-Antarctic waters during the whaling period, foraging primarily on zooplankton between spring and autumn (Kawamura 1980; Allison 2016). Although present-day diets of fin and sei whales at SGSSI remain unknown, historic stomach contents analyses indicate that fin and sei whales both consumed Antarctic krill (*Euphausia superba*) within SGSSI waters during the commercial whaling period (Matthews 1938; Brown 1968). Despite sharing a common prey resource (at least during the twentieth century), the mechanisms facilitating the coexistence of fin and sei whale consumption of Antarctic krill at SGSSI during the twentieth century and present day are unknown.

Historically, resource use has been investigated using stomach contents analysis; however, this approach is limited to a single point in time and will ultimately reflect prey availability at the time of the whale’s capture; therefore, studies using stomach contents may only provide partial information on diet (Votier et al. 2003; Bowen and Iverson 2012). In contrast, stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen

($\delta^{15}\text{N}$) provide a powerful alternative to stomach contents analysis, as they reflect prey consumption during the period of tissue synthesis. However, stable isotope analysis of animal tissues does not often provide information on specific prey species, although it can provide relative information on the resource use of marine predators within an ecosystem.

Stable isotope analysis has been widely used to study animal diets in the wild (Hobson 1999; Rubenstein and Hobson 2004; West et al. 2006), including baleen whales (e.g. Newsome et al. 2010a; Borrell et al. 2012; Eisenmann et al. 2016; Valenzuela et al. 2018; Reiss et al. 2020)), with a particular focus on carbon and nitrogen stable isotope ratios. As energy flows through an ecosystem and is passed up the food chain, carbon isotopic values ($\delta^{13}\text{C}$) can be used to determine the source of primary production within a food web (Fry 1989). As these sources differ somewhat systematically between habitats and regions, carbon isotopic values can provide a proxy for: (i) latitudinal distributions, with lower $\delta^{13}\text{C}$ towards the polar regions; (ii) foraging distance from shore, as inshore benthic food webs differ predictably in baseline $\delta^{13}\text{C}$ due to their detrital origin compared with offshore pelagic food webs; and (iii) foraging in deeper waters, with higher $\delta^{13}\text{C}$ values at increasing depth (Francois et al. 1993; Hobson et al. 1994; Cherel and Hobson 2007; Linnebjerg et al. 2013; Espinasse et al. 2019; Michel et al. 2020). Nitrogen isotopic values ($\delta^{15}\text{N}$) provide information on trophic positioning with higher $\delta^{15}\text{N}$ ratios occurring predictably up the food web (Schoeninger and DeNiro 1984; Wada et al. 1991; Boecklen et al. 2011; Healy et al. 2017), although the underlying physiological mechanisms driving this pattern are currently not fully understood (O'Connell 2017).

To better understand changes in species diet and resource use over time, historic baseline information on diet and resource use (often inferred from isotopic analysis) can be included to identify species responses to ongoing anthropogenic impacts and global environmental change (Visser and Both 2005; McClenachan et al. 2012; Clavero 2014). Isotopic information is retained in tissues post-mortem, with patterns stable over millennia, enabling the use of historic specimens to infer the resource use patterns of populations in the past (e.g. Zenteno et al. 2015). Baleen whales have multiple layers of tightly packed keratinous plates (baleen) surrounding the inner mouth edge that grow continuously from the gumline and are metabolically inert once synthesised (Rita et al. 2019) making baleen a good candidate tissue for studying temporal changes of baleen whale resource use. Indeed, isotopic analysis of incremental samples along the growth axis of baleen plates has been used to determine changes in whale foraging preferences through time (Best and Schell 1996; Trueman et al. 2019; Reiss et al. 2020).

To better understand habitat and resource use of wild populations, stable isotopes are often paired with spatiotemporal occurrence data (e.g. Robillard et al. 2021; Leal and

Bugoni 2021). Historic information on the distribution of whale species can be inferred from the timing and location of twentieth-century whaling catches (e.g. Clapham et al. 2004; Reeves et al. 2004). Shore-based whaling occurred at the island of South Georgia (within the SGSSI management area) between 1904 and 1965 and pelagic boat-based whaling started in the 1920s and continued until 1976 (Tønnessen and Johnsen 1982; Headland 1992; Allison 2016). South Georgia has been described as an epicentre of twentieth-century whaling (Jackson et al. 2020), with 8.6% of the 2.1 million whales harvested across the Southern Hemisphere taken from this region (Allison 2016). Whaling catch records are available for approximately 98,000 fin whales and 16,000 sei whales within the SGSSI EEZ (Allison 2016). Present-day population size and levels of population recovery for fin and sei whales are currently unknown in the South Atlantic, and very little ecological data from present-day populations are available.

Here, using temporal and spatial information on fin and sei whale distribution from historic whaling catches, alongside, stable isotope analysis of incremental samples from six keratinous baleen plates collected from unique individuals and discarded during the twentieth-century whaling period, we investigate resource use and partitioning of fin whales and sei whales at SGSSI during the commercial whaling period. This information may help to infer the ecological role of fin and sei whales at SGSSI and identify evidence for interspecific resource partitioning.

Materials and methods

Spatial and temporal co-occurrence inferred from whaling catches at SGSSI

Whaling catches between 1904 and 1976 were obtained from the IWC catch database version 6.1 (Allison 2016) and used to provide information on the location of species-specific catches within the boundaries of the SGSSI EEZ. Spatiotemporal correlations in the locality and timing of whaling catches of fin and sei whales were used to investigate interspecific differences in spatial and temporal use of the marine environment around SGSSI.

Stable isotope analyses

Baleen plates (fin whales, $n=3$; Sei whales, $n=3$) were collected by individual researchers between 1970 and 1974 from the shorelines of Grytviken whaling station, South Georgia (54.3° S, 36.5° W), and samples were stored at room temperature prior to sampling. Plates were collected prior to international enforcement of regulations by the Convention on International Trade in Endangered Species of

Wild Fauna and Flora (CITES) in 1975; no CITES permits are associated with these materials. Baleen was subsampled using a 10 mm metal revolving belt punch from the part closest to the gum line, subsamples cleaned using a steel wool pad and 100% ethanol, and DNA extracted following the extraction protocol by Dabney et al. (2013) in the ancient DNA laboratory at the University of Cambridge (Dept. of Archaeology). Mitochondrial control region sequences were amplified using PCR and sequences compared against NCBI reference sequences to identify species. All mitochondrial haplotypes were unique to each baleen plate, thereby verifying that each belonged to a unique individual. PCR primers and amplification details are presented in supplementary Table S1.

Baleen growth rates were reviewed in the literature to ensure that, where possible, baleen samples were representative of a minimum period of one year [> 18 cm for fin whales (Bentaleb et al. 2011), > 16 cm for sei whales (Reiss et al. 2020)]. Plates were sampled incrementally along the longest axis every 1 cm using a metal revolving belt punch with 5 mm diameter. In total, 57 incremental samples were taken from sei whales ($n=3$ plates, with 18, 19 and 20 increments per plate) and 54 from fin whales ($n=3$ plates, with 15, 19 and 20 increments per plate).

Lipids were removed by alternating 2:1 chloroform/methanol mixture and 2:1 methanol/chloroform mixture whilst soaking in an ultrasonic bath, changing the solvent every 30 min until the solution remained clear; the number of washes varied across increments (range: 1–3). Carbonates were removed through demineralization in 0.5 M aq. hydrochloric acid and extracts rinsed using triplicate washes of deionised H_2O . Samples were then freeze-dried and weighed (mean \pm SD, 0.8 ± 0.1 mg) in triplicate into tin capsules. Stable isotope ratios of carbon and nitrogen were measured using a Costech Elemental Analyser coupled with a Thermo Delta V Plus continuous flow stable isotope mass spectrometer (EA-IRMS), at the Godwin Laboratory, Department of Earth Sciences, University of Cambridge. Replicate analyses of international standards were used to correct for instrumental drift. Carbon and nitrogen stable isotope values are expressed as delta values (δ) relative to international standards (Vienna PeeDee Belemnite— $\delta^{13}C$ and atmospheric N_2 — $\delta^{15}N$; see (Hoefs 2018)). Repeated measurements of in-house standards (caffeine, nylon, alanine, protein 2) were used to determine measurement precision ($\delta^{13}C$ —0.1, $\delta^{15}N$ —0.2).

Mass spectrometry results were retained for analysis if they passed the following quality control (QC) checks: (i) atomic carbon/nitrogen ratio (C:N hereafter) remained at approximately 3.4 (± 0.5) (see: O'Connell and Hedges 1999; O'Connell et al. 2001; Newsome et al. 2010b; Bentaleb et al. 2011; Ryan et al. 2013), and (ii) lipids were removed successfully (accidental retainment of lipid was assessed using

correlation between $\delta^{13}C$ and C:N (Post et al. 2007)). Triplicate repeats of incremental $\delta^{13}C$ and $\delta^{15}N$ were averaged prior to data analysis.

Data analysis

All analyses were performed using software R version 4.0 (RStudio Team 2020), and maps created using open-source geospatial software, qGIS version 3.10.13 (Quantum 2017).

Spatial and temporal co-occurrence inferred from whaling catches at SGSSI

Spatial patterns To enable comparison of species-specific distributions whilst accounting for interspecific differences in the relative abundance inferred from catch data, whaling catch densities were mapped into 72 equal sized hexagonal bins and percentiles calculated using the quantile function in R (version 4.0). Each hexagonal bin spanned two decimal degrees longitude and latitude across the SGSSI EEZ, and catches were summed within each bin. A correlation coefficient of spatial association (Clifford et al. 1989; Dutilleul et al. 1993) was used to infer similarities in distribution (spatial partitioning) between fin and sei whales within the SGSSI EEZ using the “modified.ttest” function in the package SpatialPack (Osorio et al. 2014). This coefficient measures the amount of correlation between two spatial sequences (in this case, the distribution of whaling catches of fin and sei whales), with values close to 0 representative of no spatial correlation and values close to 1 representative of complete spatial correlation.

Temporal patterns Monthly catch rates were calculated for each species (total catches that occurred within the SGSSI EEZ between 1904 and 1976 per month) and the similarity in the peak timing of catches was compared using a cross-correlation analysis. Cross-correlation measures the similarity of two time series, whereby two identical (or almost identical time series) will display a peak at zero (Derrick and Thomas 2004). Cross-correlations were performed using the “ccf” function in the ‘base’ stats package in R and a significant correlation assessed using critical values at the 5% level (R Development Core Team 2003); a significant value of +1 or higher would resemble significant lag in the peak timing of catches of one or two months, respectively.

To identify whether variation in whaler behaviour throughout the commercial whaling period [e.g. whalers foraging inshore or offshore; whaler preference for a particular species at a given time (fin whales: 1937–1965; sei whales: 1965–1975)] may have resulted in spatiotemporal variation in the occurrence of fin and sei whales at SGSSI, catch data were binned into three time periods (early: 1904–1928; middle: 1929–1952; late: 1953–1976). We then compared

interspecific differences in temporal (cross-correlations) and spatial (modified *t* tests) catch patterns within and between each time period analysed.

Measuring historic resource partitioning using stable isotope analysis

Interspecific variation The Mann–Whitney *U* test (MacFarland and Yates 2016) was used to identify statistical differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between fin and sei whales as inference of variation in resource use between these two species. A nonparametric test was used as the assumptions of residual normality and homogeneity of variance were violated (Shapiro Wilk's and Levene's test, respectively).

The ecological niche space of fin whale and sei whale was inferred from pairwise values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from baleen plates under a bivariate normal distribution (ellipses of multivariate δ -space are commonly used for ecological applications (Newsome and Martinez del Rio 2007; Newsome et al. 2010a, b). Multivariate δ -space of fin whale and sei whale at SGSSI was estimated using two models: (i) using maximum likelihood estimates corrected for small sample sizes (SEA_C) and (ii) using Bayesian estimates of isotopic niche space (SEA_B), both calculated using the R package SIBER (Jackson et al. 2011). To identify isotopic evidence for resource partitioning, percentage overlap of niche space between fin whales and sei whales was measured using the `bayesianOverlap` function from the R package SIBER (Jackson et al. 2011). Niche size and overlap were measured twice for both models (SEA_C and SEA_B). First, only incorporating c.40% (reflecting the core trophic niche) and second using c.95% (reflecting the full trophic niche), following Jones et al. (2020). SIBER uses a Markov chain Monte Carlo (MCMC) model-fitting algorithm. MCMC parameters were as follows: 100,000 iterations, 1000 burn-in, 5% thinning and 3 independent chains. Coherence among chains were determined for each model parameter using a Gelman–Rubin diagnostics of < 1.1 (Gelman and Rubin 1992; Brooks and Gelman 1998). Species differences in SEA_B were compared by assessing overlap of 95% credible intervals of posterior distributions (95% CIs). Differences were deemed statistically significant if 95% CIs did not overlap. Graphical ellipses were drawn using the `plotSiberObject` function in the R package SIBER.

As multiple measurements were made for each individual (i.e. along the baleen), the assumption of complete independence of data points was violated. To overcome this, additional datasets were created by randomly subsampling ten data points from each of the six individuals ($n = 60$) without replacement 200 times. For each subsampled dataset ($n = 200$) the Breusch–Godfrey test (Breusch 1978) was used to detect autocorrelation between the residuals (per plate) and removed if significant. For

the remaining subsampled datasets ($n = 96$), the replicated analyses provided similar results to the full dataset (assessed by comparing overlap of 95% CIs of posterior distributions). This suggests that pseudoreplication was not biasing the results (see supplementary Table S4, Figure S7). Therefore, results based on the full dataset are presented in subsequent sections.

Intraspecific variation Within species, similarity of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from incremental baleen samples for each individual was assessed by comparing overlap of posterior distributions. Posterior distributions were calculated using SIBER (95% CIs), and differences were deemed significant if 95% CIs did not overlap.

Results

Spatial and temporal co-occurrence inferred from whaling catches at SGSSI

Totals of 16,400 sei whales and 98,843 fin whales were caught within the boundary of the South Georgia and South Sandwich Islands EEZ between 1904 and 1976; location of EEZ is shown in Fig. 1. Fin whales were caught year-round, predominantly between September and May with the highest catches totalling 19,821 (20.1% of all fin whale catches within the SG EEZ) and 28,045 (28.4%) in December and January, respectively (Fig. 2; Table S2). Sei whales were caught from November–May, with the highest catches occurring from February–March (36.4% and 38.7% of all sei whale catches within the SGSSI EEZ, respectively) (Fig. 2; Table S2).

Intraspecific spatial patterns

Within fin whales, significant differences in the spatial distribution of catches were observed between all time periods (Fig. S4, Table S4). The mean tendency of fin whale catches was at slightly lower latitudes during the early whaling period (< 1929) relative to the mid (1930–1951) to late time periods (> 1952) (Fig. S4). Within sei whales, a significant difference was observed in the spatial distribution of catches between the middle and late time periods (Fig. S4, Table S4). As all sei whale catches occurred within a single hexbin during the early whaling period, correlations between the early time period and later time periods could not be formally tested (Fig S4, Table S4). Sei whales were caught inshore at South Georgia and offshore at lower latitudes within the SGSSI EEZ during the mid (1929–1952) to late (1953–1976) time periods (Fig. S4).

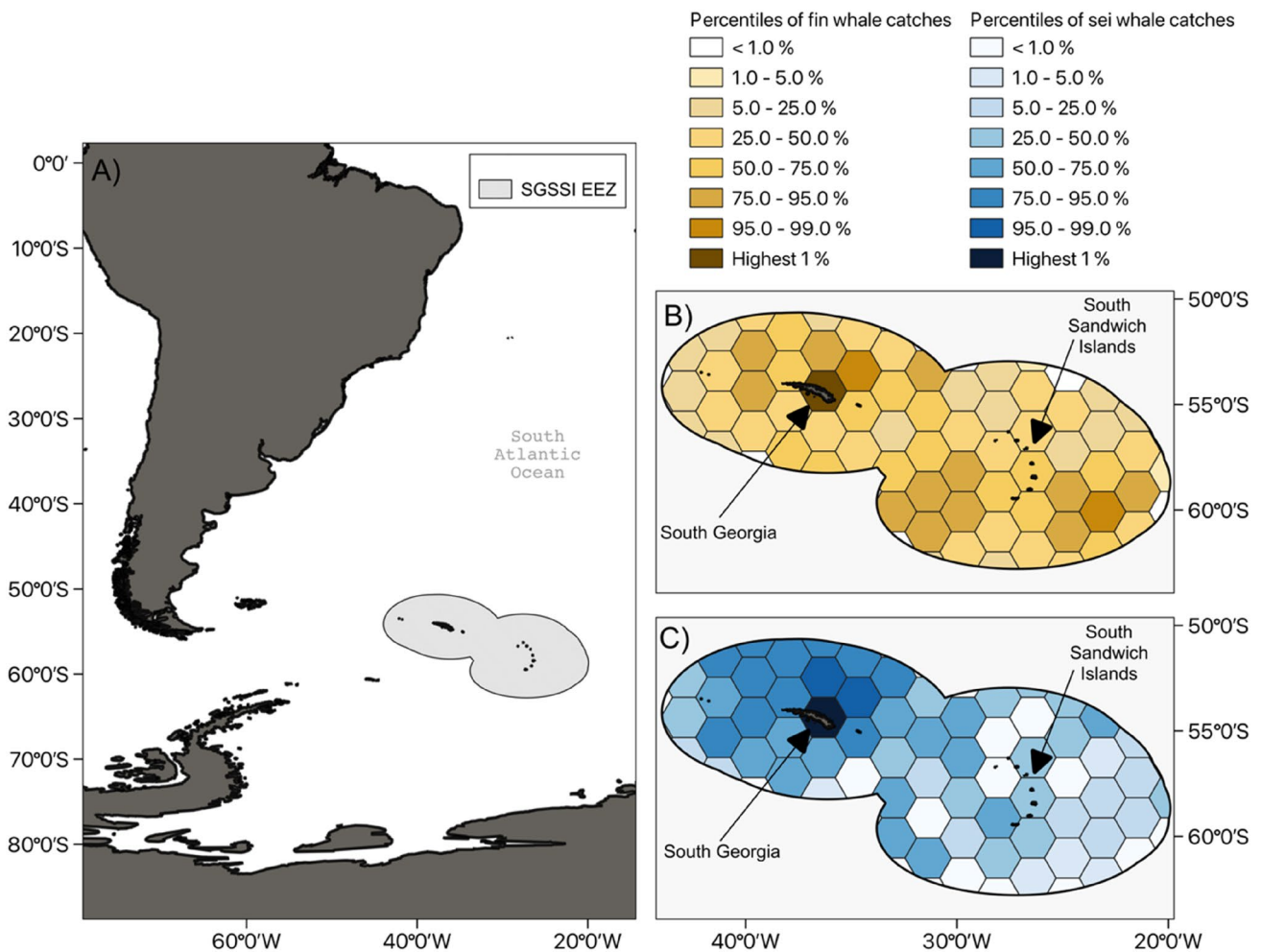


Fig. 1 A Location of South Georgia Exclusive Economic Zone (EEZ), South Atlantic, in relation to the Sub-Antarctic Front (dashed line), Polar Front (solid line), and Southern Antarctic Circumpolar

Current (dot-dash line). Spatial distribution of fin **B** and sei **C** whale catches within the South Georgia Exclusive Economic Zone between 1904 and 1976

Interspecific spatial patterns

The overall catch distributions significantly differed between the two species within the SGSSI EEZ (Correlation coefficient close to zero, $t=0.008$, $F=0.01$, $df=1, 188$, $p=0.91$; Fig. 1). Fin whales were caught across the entire EEZ, with the highest catches recorded close to the island of South Georgia, where the whaling stations were established (Fig. 1). Moderate levels of fin whale catches were also recorded in offshore waters surrounding the island of South Georgia and at a band approximately -59 degrees latitude, towards the lower half of the South Sandwich Islands. Similarly, to fin whales, the highest numbers of sei whale catches were recorded close to the island of South Georgia (Fig. 1). However, in contrast to fin whales, sei whales were caught predominantly at lower latitudes with the percentile of catches much lower at higher latitude regions (e.g. near to the South Sandwich Islands).

Intraspecific temporal patterns

Within species, cross-correlations showed no significant differences in the peak timing of fin whale catches over time, with the highest numbers of fin whales caught in January, consistent across time periods (Table S3, Fig. S3. A–C). Prior to 1929, there were fewer catches of fin whales recorded during the austral winter (June to September) relative to the rest of the year, and no winter catches after 1929 (Table S3, Fig. S2). For sei whales, the highest numbers of catches occurred between February and April and peak catch times remained relatively consistent across time periods (Table S3, Fig. S2–S3). A significant difference was observed between the early whaling period (highest in March and April) relative to the middle and late whaling periods (highest in February and March) (Fig. S3.D, E, respectively). No sei whale catches were reported during winter (June to September), and relatively few sei whale

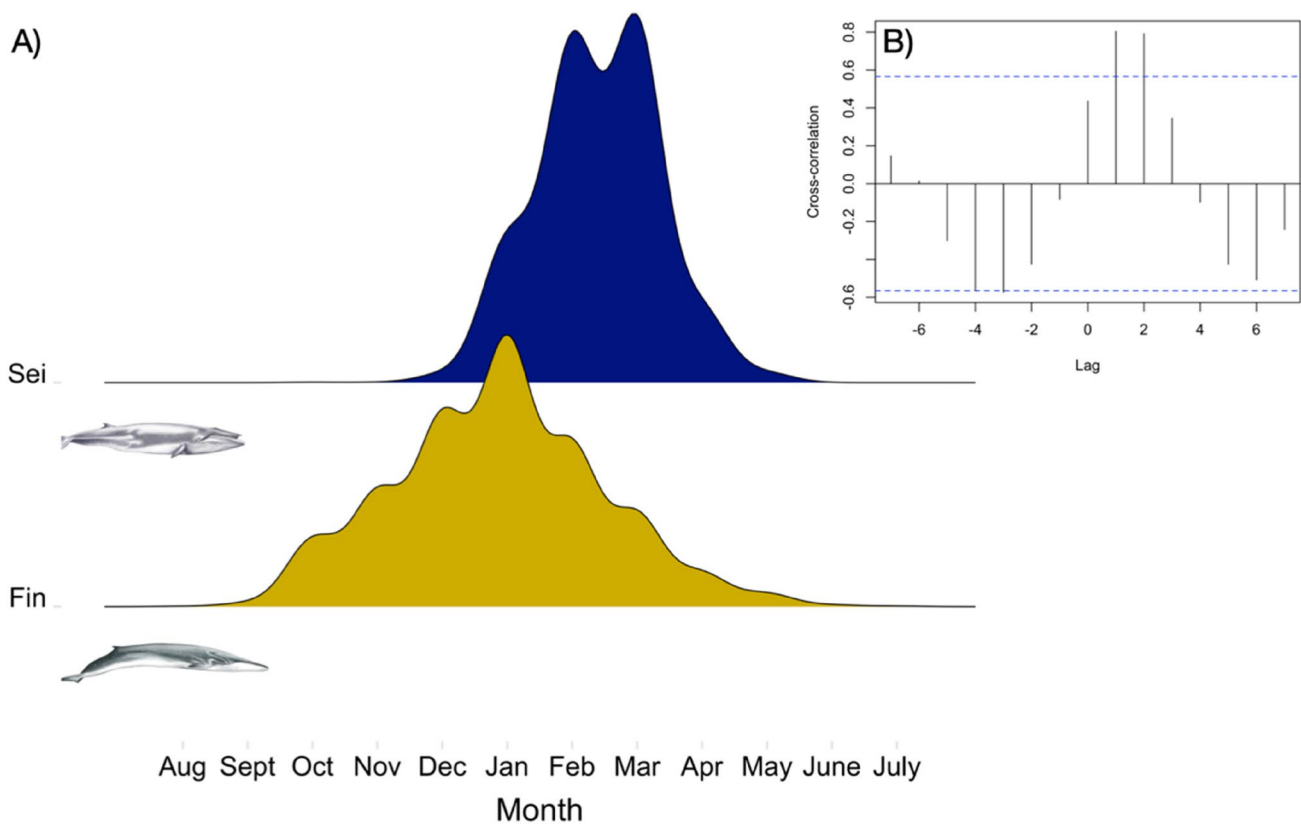


Fig. 2 A Density distributions of monthly commercial catches of sei whale (blue) and fin whale (orange) within the South Georgia Exclusive Economic Zone between 1904 and 1976. **B** Cross-correlation

functions graphically representing the monthly lag time of sei whale catches compared with fin whale catches. Blue dotted line represents the line of statistical significance at $p=0.05$

catches were made between October and December, consistent across time periods (Table S3, Fig S2–S3).

Interspecific temporal patterns

Throughout the twentieth century, the peak timing of fin whale catches occurred earlier in the season at the SGSSI EEZ compared with sei whales. This was supported by cross-correlation functions which indicated that the peak timing of sei whale catches was at least one month later relative to fin whales (statistically significant lag time of one to two months, Fig. 2, ccf: +0 – 0.436, +1– 0.792, +2 0.804).

Temporal patterns of peak catches were consistent within time periods, with peak fin whale catches occurring earlier in the season compared with sei whales during the early, mid and late whaling periods. (Fig. S2). This was supported by cross-correlation functions with a statistically significant lag time in peak catches between 1 and 3 months depending on time period (Fig. S3). Prior to 1929, the significant lag time was two to three months (Fig. S2, ccf: +2– 0.666, +3– 0.599, $p < 0.05$). In contrast, both the middle (1929–1953) and late catch periods (> 1953) had significant lag times of one to two

months (Middle ccf: +1– 0.783, +2– 0.846, Fig. S2; Late ccf: +1– 0.683, +2– 0.747, Fig. S2, $p < 0.05$).

Inference of historic resource partitioning using stable isotope analysis

Stable isotope ratios were successfully measured in 111 baleen samples from sei whales ($n=3$ plates, with 18, 19 and 20 incremental samples) and fin whales ($n=3$ plates, with 15, 19 and 20 incremental samples). Within plates, no correlation was observed between $\delta^{13}\text{C}$ and C:N suggesting that residual lipids had been removed appropriately (Fig. S1).

Intraspecific variation

Minimum and maximum $\delta^{13}\text{C}$ values were varied within fin whales (-20.7‰ to -20.2‰ ; -23.1‰ to -21.5‰ ; -21.3‰ to -17.4‰) and similar within sei whales (-19.7‰ to -16.7‰ ; -21.1‰ to -16.9‰ ; $-19.9.1\text{‰}$ to -14.3‰) (Fig. 3). Minimum and maximum $\delta^{15}\text{N}$ values were similar within sei whales (7.8‰ to -9.3‰ ; 7.8‰ to 10.0‰ ; 7.7‰ to 10.2‰) and within fin whales (6.3‰ to 7.1‰ ; 6.0‰ to 7.6‰ ; 6.5‰ to 7.9‰)

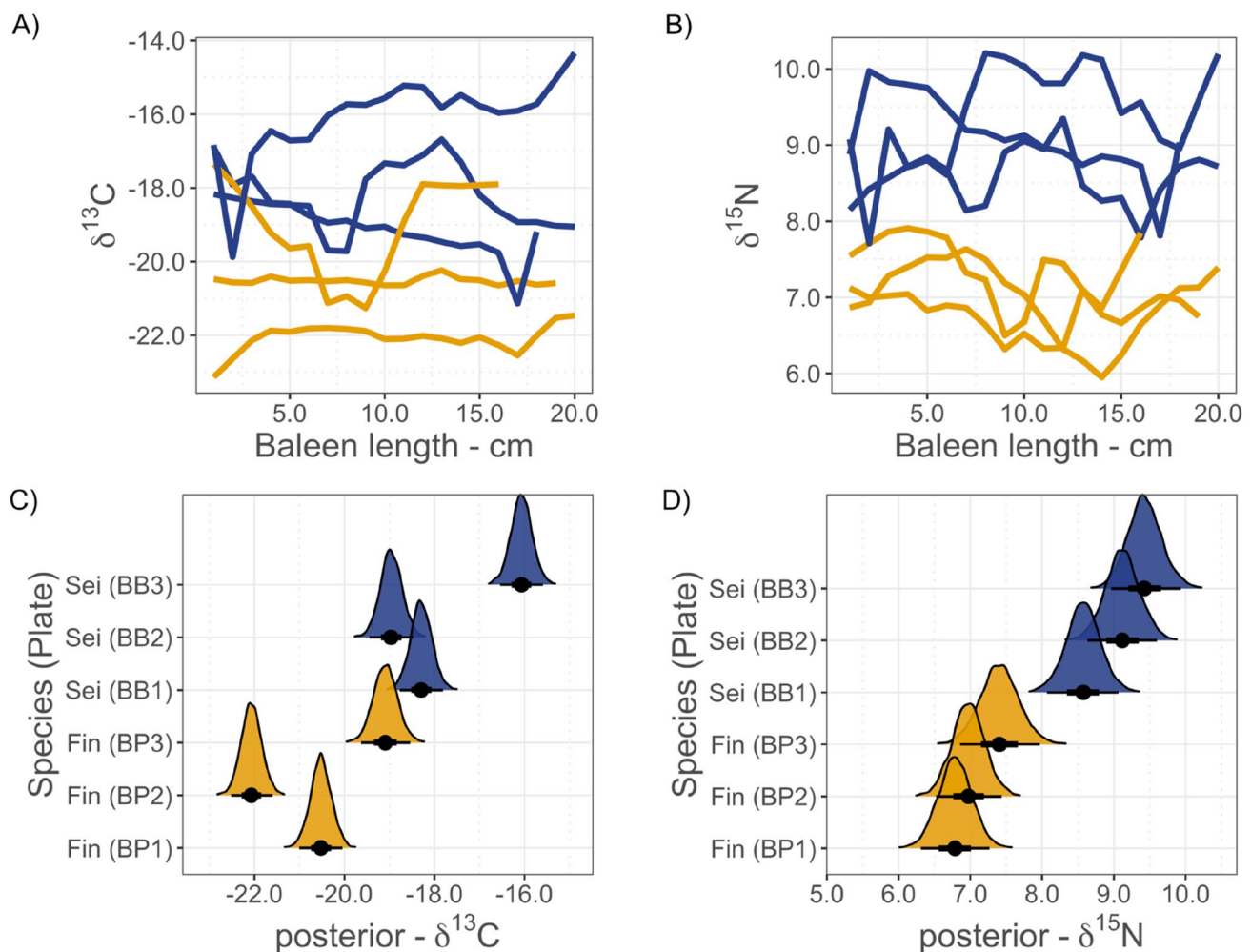


Fig. 3 **A** Variation in $\delta^{13}\text{C}$ values of incremental samples from baleen plates of fin whale (orange) and sei whale (blue). **B** Variation in $\delta^{15}\text{N}$ values of incremental samples from baleen plates of fin whale (orange) and sei whale (blue). Youngest to oldest samples are presented from left to right with samples at zero cm close to the gum-

line. Posterior distributions of stable isotope ratios **C** $\delta^{13}\text{C}$ values; and **D** $\delta^{15}\text{N}$ values of fin whale *Balaenoptera physalus* (orange) and sei whale *Balaenoptera borealis* (blue) baleen collected at South Georgia during the early 1970s extracted from SIBER analysis. Significant differences were assessed by overlap of the 95% credible intervals

(Fig. 3). Within species, differences in $\delta^{15}\text{N}$ values between individuals were minimal, with significant overlap of 95% CIs (Fig. 3, Table S5). In contrast, significant intra-specific variation of $\delta^{13}\text{C}$ was observed between one individual and the other two individuals, consistent for both species (Fig. 3, Table S5). However, posterior distributions from SIBER analysis do not capture the full variation in $\delta^{13}\text{C}$ and at least some incremental samples along the annual growth cycle overlapped in $\delta^{13}\text{C}$ within species (Fig. 3, Fig. S5).

Interspecific variation

Sei whale baleen showed significantly higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compared to fin whale baleen ($\delta^{13}\text{C}$: $W = 263$, $p < 0.001$; $\delta^{15}\text{N}$: $W = 13$, $p < 0.001$; Fig. 4). Across all incremental sei whale samples, $\delta^{15}\text{N}$ values ranged from

7.7‰ to 10.2‰ (mean \pm SD: 9.1 ± 0.6 , $n = 57$), and $\delta^{13}\text{C}$ values ranged from -21.1‰ to -14.3‰ (mean \pm SD: -17.7 ± 1.6 , $n = 57$). In contrast, across all incremental fin whale samples, $\delta^{15}\text{N}$ values ranged from 5.9 to 7.9‰ (mean \pm SD: 7.03 ± 0.48 , $n = 54$), and $\delta^{13}\text{C}$ values ranged from -23.1‰ to -17.4‰ (mean \pm SD: -20.7 ± 1.4 , $n = 54$, Fig. 4, Table 1).

Sei whale niche area, measured as standard ellipse area, was larger than fin whales ($\% \pm \text{SD}$: 3.4 ± 0.3 , 2.7 ± 0.2 , respectively), consistent across 40% and 95% ellipse contours and across maximum likelihood (SEAc) and Bayesian estimates (SEAb) (Fig. 4, Table 2). No overlap in isotopic niches was observed at the core niche level (c.40%) and approximately 9% of overlap was observed when ellipse areas were estimated using 95% of the data (Table 2).

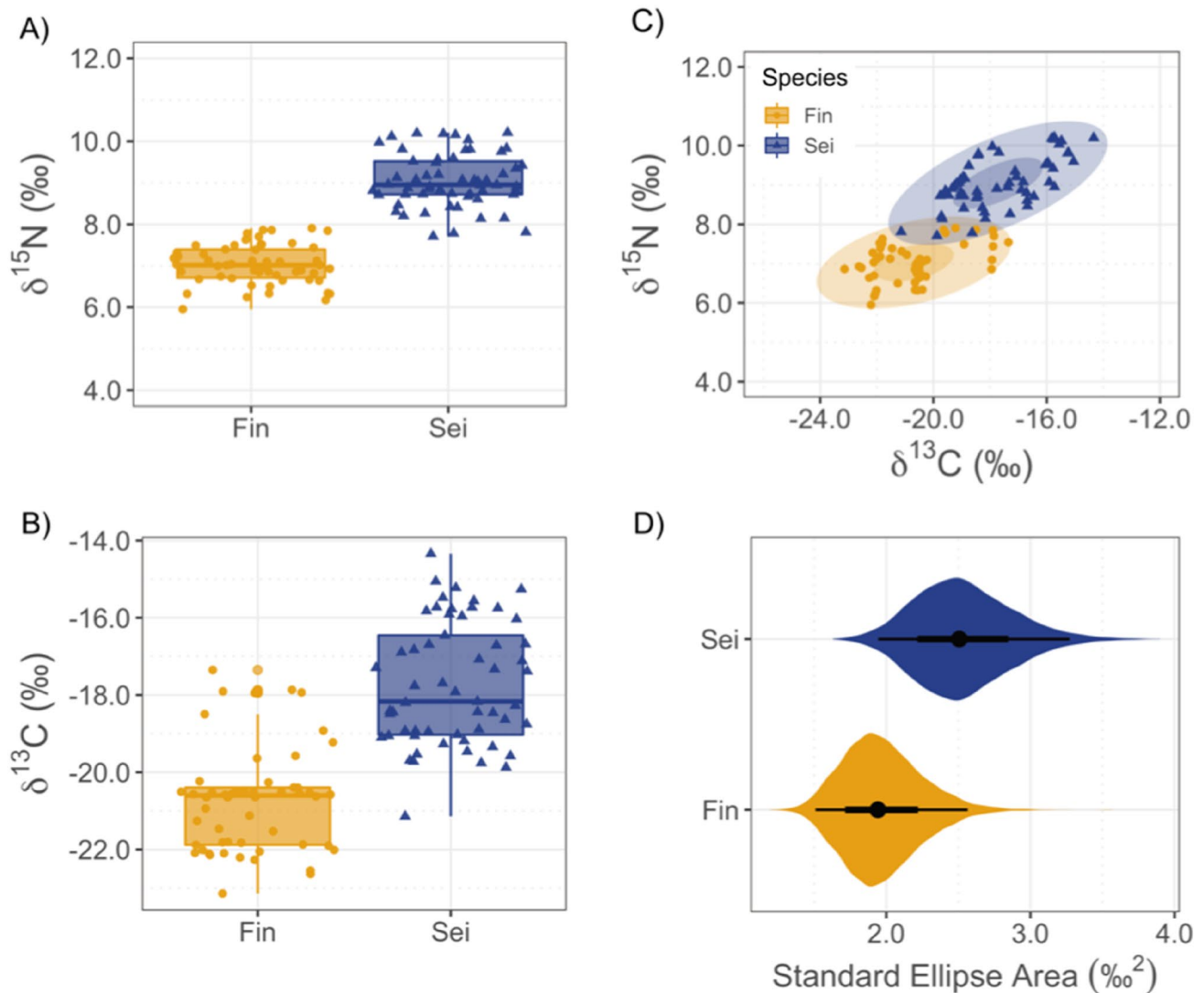


Fig. 4 **A** $\delta^{15}\text{N}$ values and **B** $\delta^{13}\text{C}$ values of fin whale (orange circles) and sei whale (blue triangles) baleen collected from ex-whaling sites at South Georgia during the early 1970s. **C** Bivariate stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of incremental baleen samples from fin whale (orange circles) and sei whale (blue triangles) collected at South

Georgia during the early 1970s. Bivariate ellipse areas representing 40% (inner contour) and 95% (outer contour) of the data are shown. **D** Posterior distributions and 95% credible intervals (thin black line) of fin whale (orange) and sei whale (blue) Bayesian standard ellipse areas from SIBER analysis (SEAb)

Discussion

Our study is the first to show evidence of interspecific resource partitioning by baleen whales in the Southern Hemisphere during the twentieth-century whaling period using multiple lines of evidence and is the first study using isotopic data to measure resource partitioning between whale species on a summer feeding ground in the South Atlantic. Here, by comparing the spatiotemporal occurrence of fin and sei whales within the SGSSI EEZ during the twentieth century, we showed that sei whales may have occurred at SGSSI later in the season relative to fin whales and that sei whales predominantly utilised the northern

part of the EEZ, whilst fin whales were more widely distributed. Historic baleen specimens from the sub-Antarctic during the commercial whaling period are rare; therefore, our sample sizes for isotopic analysis were small (111 incremental samples from 6 individuals). Although confidence in our isotopic results is limited by small sample sizes, the distinct isotopic niches of fin and sei whales when combined with the spatiotemporal differences from catch data provide novel insight into how resource partitioning may have facilitated the coexistence of fin and sei whales at SGSSI during the twentieth-century whaling period.

Table 1 Mean (\pm SD) stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of baleen plates sampled from individual fin whale, *Balaenoptera physalus*, and sei whale, *Balaenoptera borealis* in the 1970s at South Georgia, South Atlantic

Species	Specimen ID	<i>n</i> (cm)	Collection	Collection Year	$\delta^{13}\text{C}$ ‰ (\pm SD)	$\delta^{15}\text{N}$ ‰ (\pm SD)
Sei	BB1	20	BAS	1970	- 16.1 (1.1)	9.4 (0.7)
	BB2	18	BAS	1970	- 18.9 (0.9)	9.1 (0.5)
	BB3	19	BAS	1972	- 18.3 (0.9)	8.6 (0.4)
Mean		57			- 17.7 (1.6)	9.1 (0.6)
Fin	BP1	15	BAS	1970	- 19.1 (1.3)	7.4 (0.5)
	BP2	19	Private collection—BH	1974	- 20.5 (0.1)	6.7 (0.3)
	BP3	20	Private collection—BH	1974	- 22.1 (0.3)	7.0 (0.5)
Mean		54			- 20.7 (1.4)	7.0 (0.5)

Baleen plates are currently stored at the British Antarctic Survey biological specimen store (BAS) and from one private collection (Bob Headland, BH). *n*—the number of incremental samples taken per plate

Interspecific resource partitioning in baleen whales

Here, whaling catch data demonstrated that fin whales were caught year-round at SGSSI, with highest catches during December and January. Comparatively, sei whales were only caught between January and May with highest catches between February and April. This pattern was consistent across time periods (early, middle, late), with the majority of fin whale catches earlier in the season compared with sei whales. Additionally, sei whales were predominantly caught in the northern part of the EEZ, whereas fin whales were caught throughout the region. Both species co-occurred in the late summer and early autumn during the twentieth century within the SGSSI EEZ, which may have increased competition.

Although no study has examined the contemporary spatiotemporal occurrence of fin and sei whales at SGSSI, both species co-occur on feeding grounds in other parts of the globe (Flinn et al. 2002; Frans and Augé 2016; Silva et al. 2019; Buchan et al. 2021; García-Vernet et al. 2021). For

example, off the coast of the Falkland Islands in the western South Atlantic, fin and sei whales were both historically observed by local inhabitants predominantly between January and June (Frans and Augé 2016). The Falkland Islands are known feeding grounds for sei whales (Segre et al. 2021); however, limited information is available for fin whales in this region and sightings are rare (GBIF 2021). In the North Pacific, fin and sei whales are observed during summer off the coast of British Columbia; however, sei whales are observed further offshore, likely associated with the abundance and distribution of copepods, whilst fin whales are associated with the availability of euphausiids (Flinn et al. 2002). In the North Atlantic, fin and sei whales co-occur on winter feeding grounds in the Azores (Silva et al. 2019) and similarly to our study, using isotopic niches Silva et al. (2019) showed that present-day populations of fin and sei whales partition resources in the North Atlantic. These examples demonstrate that fin and sei whales co-occur on feeding grounds across the globe.

Despite the seasonal co-occurrence of fin and sei whales at SGSSI, no overlap of the ‘core’ niche (c.40%) and only partial overlap of the entire niche (c.95%) was observed between the fin and sei whales using stable isotope analysis in our study, suggesting that these sympatric species may have partitioned resources on South Atlantic feeding grounds. Resource partitioning has been observed for other sympatric baleen whale species across the globe, including other whale feeding ground sites in the Southern Ocean (Friedlaender et al. 2009; Ryan et al. 2013; Sasaki et al. 2013; Gavrilchuk et al. 2014; Witteveen and Wynne 2016; Herr et al. 2016; Seyboth et al. 2018; Silva et al. 2019; Milmann et al. 2020; Mansouri et al. 2021). For example, Seyboth et al. (2018) found evidence for resource partitioning among fin, humpback, and minke whales on a summer polar feeding ground at the western Antarctic Peninsula (~ 15 degrees further South relative to South Georgia). To date, very few isotope studies have included sei whales (Sasaki

Table 2 Interspecific niche attributes estimated using SIBER (Jackson et al. 2011)

Niche attribute:	Species:	
	Sei mean (SD)*	Fin mean (SD)*
SEAc (%c2)*	2.5	2.0
SEAb (%c2)	2.5 (1.9–3.2)	1.9 (1.5–2.5)
Core niche overlap (%) (40% contour)	0.0 (0.0–0.0)	0.0 (0.0–0.0)
Full niche overlap (%) (95% contour)	9.2 (0.8–19.1)	9.4 (0.8–18.5)

Maximum likelihood estimates of bivariate ellipses of isotopic niche area ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) corrected for small sample sizes (SEAc). Mode and 95% credible intervals of Bayesian estimates of the isotopic niche area (SEAb). Percentage overlap of bivariate isotopic niche areas (SEAp) using the core niche (c.40%) and the full niche (c.95%)

et al. 2013; Silva et al. 2019) with no multispecies studies published from the Southern Hemisphere.

Sei whales have been observed foraging at lower latitudes elsewhere in the South Atlantic, including coastal Africa (Best 1967; Best and Gambell 1968; Best and Lockyer 2002). In our study, all three sei whales had much higher $\delta^{13}\text{C}$ across the majority of their incremental samples compared with fin whales, consistent with foraging at lower latitudes across the year (as lower $\delta^{13}\text{C}$ values occur nearer the poles, see Cherel and Hobson 2007; Magozzi et al. 2017; Espinasse et al. 2019). Moreover, the distribution of whaling catches circumpolar suggest sei whales foraged across a lower latitudinal range relative to fin whales in the Southern Hemisphere, with fin whales reported at both sub-polar and polar latitudes, and adult sei whales only occasionally reported at polar latitudes (Mizroch et al. 1984; Mizroch and Rice 1984; Horwood 1987; Kasamatsu 1996, 2000). This pattern was reflected by the catch data presented in our study with sei whales occurring predominantly within the northern part of the SGSSI EEZ, whilst fin whales occurred throughout; therefore, the higher $\delta^{13}\text{C}$ across the majority of sei whale samples may have been due to relatively lower latitude foraging by sei whales in sub-polar habitats.

It is important to note that our results were based on 111 incremental baleen samples from only six individuals (3 fin, 3 sei), and therefore, further samples would be required to interpret the observed patterns in a population context. Nevertheless, historic whale specimens from the Southern Ocean are rare and dietary information for fin and sei whales is currently extremely limited at SGSSI; therefore, our study provides novel information on historical foraging strategies in these two species for an understudied part of the Southern Ocean, known to represent vital whale feeding habitat (Atkinson et al. 2001; Jackson et al. 2020). Further isotopic information on fin and sei whales in the Southern Ocean will help to determine whether these two sympatric species still co-occur and partition resources at SGSSI and how they may partition resources with other Balaenoptera whale species.

Foraging ecology of krill predators at South Georgia

South Georgia is well known for its iconic marine megafauna associated with high levels of primary productivity and dense aggregations of zooplankton. Many penguin, fish, seal, and seabird colonies inhabit the region with somewhat overlapping diets, many of which forage on Antarctic krill (Bearhop et al. 2006; Phillips et al. 2011; Waluda et al. 2017; Horswill et al. 2018; Jones et al. 2020; Mills et al. 2020, 2021; Hollyman et al. 2021). Direct information on fin and sei whale diet is limited to studies that reported stomach contents during the commercial whaling period. These studies suggest fin whales fed predominantly on euphausiid krill across the Southern Ocean (Mackintosh and Wheeler 1929; Mackintosh 1942; Nemoto and Nasu 1958; Nemoto 1959; Kawamura 1980), whilst sei whales had a broader diet, including copepods, amphipods, and decapods (Nemoto 1959; Nemoto 1962; Klumov 1963; Brown 1968; Nemoto 1970; Kawamura 1974; Budylenko 1978). At South Georgia, fin whales and sei whales foraged on euphausiids (krill) with some evidence of sei whales supplementing the diet with amphipods at low and high latitudes during the twentieth century (Matthews 1938; Brown 1968).

Predators that forage on similar food items at the same time of year are likely to display similar stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, see Lepoint and Das 2011). In our study, stable isotope ratios of fin whale baleen (means \pm SDs: $\delta^{13}\text{C}$, -20.7 ± 1.4 ‰, $\delta^{15}\text{N}$, 7.0 ± 0.5 ‰) were similar to various present-day krill predators at South Georgia, including southern right whales (-21.0 ± 0.4 ‰, 8.2 ± 0.8 ‰), male Antarctic fur seals (-21.7 ± 1.2 ‰, 9.0 ± 1.0 ‰), gentoo penguins (-18.9 ± 0.3 ‰, 8.6 ± 0.3 ‰) and macaroni penguins (-20.0 ± 0.6 ‰, 8.9 ± 0.4 ‰), whilst sei whale values were similar albeit slightly higher ($\delta^{13}\text{C}$, -17.7 ± 1.6 ‰, $\delta^{15}\text{N}$, 9.1 ± 0.6 ‰) (Table 3). Although historic and present-day isotopic data are not directly comparable due to temporal and spatial changes in isotopic baselines (Keeling 1979; Misarti et al. 2009, 2017; Baker et al. 2010; Eide et al.

Table 3 Stable isotope values of marine predators at South Georgia

Species	$\delta^{13}\text{C}$ values	$\delta^{15}\text{N}$ values	Sample size	Period of study	Tissue	Source
Fin whale	-20.7 ± 1.4 ‰	7.0 ± 0.5 ‰	54 ^a	Early 1970s	Baleen	This study
Sei whale	-17.7 ± 1.6 ‰	9.1 ± 0.6 ‰	57 ^a	Early 1970s	Baleen	This study
Male Antarctic fur seals	-21.7 ± 1.2 ‰	9.0 ± 1.0 ‰	20 ^b	2016/17	Whiskers	Jones et al. 2020
Gentoo penguins (female)	-18.9 ± 0.3 ‰	8.6 ± 0.3 ‰	9	2002	Blood	Bearhop et al. 2006
Gentoo penguins (male)	-18.8 ± 0.4 ‰	9.1 ± 0.2 ‰	6	2002	Blood	Bearhop et al. 2006
Macaroni penguins (female)	-19.5 ± 1.0 ‰	8.9 ± 0.4 ‰	8	2002	Blood	Bearhop et al. 2006
Macaroni penguins (male)	-20.0 ± 0.6 ‰	9.3 ± 0.4 ‰	8	2002	Blood	Bearhop et al. 2006
Southern right whale	-21.0 ± 0.4 ‰	8.2 ± 0.8 ‰	2	2018	Skin	Jackson et al. 2020

^asample sizes includes repeat sequential sampling from 3 individuals

^bmeans and stdevs include repeat samples from Antarctic male fur seal individuals

2017), the similarity in isotopes between twenty-first century krill predators and twentieth-century whales (Table 3), alongside the historic diet data (Matthews 1938; Brown 1968), provide some indication that fin and sei whales may have consumed krill at South Georgia during the twentieth century. Additionally, although the lowest paired values of sei whale $\delta^{13}\text{C}$ and $\delta^{15}\text{C}$ values are similar to krill predators at South Georgia (Table 3), many of the higher sei whale $\delta^{13}\text{C}$ values (total range -21.1‰ to -14.3‰) fall outside the observed range measured for other predators. This information, combined with the short occupancy time of sei whales at South Georgia inferred from catch data, could suggest that sei whales were feeding on alternative prey sources at lower latitudes when not on the South Georgia feeding grounds. This hypothesis is supported by observations of sei whales foraging on low-trophic zooplankton at lower latitudes during winter (Best and Gambell 1968; Horwood 1987; Prieto et al. 2012; Silva et al. 2019). Further research on sei whale diet throughout their foraging range is required to understand whether sei whales are supplementing higher trophic prey at SGSSI, or whilst at lower latitudes (prior to arrival on the feeding grounds).

Intra-individual variation and evidence of winter foraging in fin and sei whales

South Georgia and the South Sandwich Islands are thought to represent a long-term (historical and contemporary) feeding ground for both species; however, there is limited information on the precise migratory routes and wintering locations for South Atlantic fin and sei whales populations that forage at SGSSI (Mackintosh 1942; Mikhalev 2020). There is some evidence to suggest that the Brazilian coast (Andriolo et al. 2010; Weir et al. 2020) and southwest coast of Africa represent wintering grounds for sei whales (Best 1967; Best and Gambell 1968; Best and Lockyer 2002; Best and Folkens 2007); and our stable isotope patterns also support the hypothesis that sei whales at South Georgia may have been feeding at low latitudes in winter (demonstrated by the higher $\delta^{13}\text{C}$ values, Fig. 3). Fin whales have also been observed off the South African coast during the austral winter (Best 1967; Best and Folkens 2007; Shabangu et al. 2019). Historically, fin whales have been thought to fast during winter on migration (Mackintosh and Wheeler 1929; Best and Folkens 2007). In our study, patterns of $\delta^{13}\text{C}$ values from one out of three fin whale plates and all three sei whale plates are consistent with winter foraging at lower latitudes, demonstrated by $\delta^{13}\text{C}$ values above -20‰ , followed by a dramatic reduction in $\delta^{13}\text{C}$ between 5 and 10 cm associated with a temporary shift towards polar feeding (Fig. 3). Indeed, acoustic detections suggest fin whales may seasonally forage on temperate krill species such as *Nematoscelis megalops* at lower latitudes in the productive Benguela

ecosystem (Shabangu et al. 2019). The other two fin whale plates in our study show consistent $\delta^{13}\text{C}$ values throughout the year (Fig. 3), suggesting they either maintain polar foraging year-round, or fast when migrating to lower latitudes. Similar patterns of intra-specific variation have been previously observed in the Southern Hemisphere for humpback whales (Eisenmann et al. 2016) and southern right whales (Rowntree et al. 2008), where some individuals fast and others forage at low latitudes. Further research is needed to establish migratory connectivity between SGSSI and lower latitude wintering grounds for fin and sei whales, and to better understand the occurrence of foraging on wintering grounds for both species.

Possible biases of whaling catch data

In this study, we observed many catches of fin and sei whales nearshore to the island of South Georgia during the early whaling period (< 1929). It is possible that these nearshore catches represent the plentiful whale numbers that occurred nearshore during this time, or, they may also reflect whalers recording catches at the time of landing, rather than at sea during incidence of capture (Tønnessen and Johnsen 1982). As whaling was predominantly close to the shoreline during the early whaling period (until steam-powered catcher vessel improved in the 1920s) and reporting generally improved throughout the twentieth-century (Tønnessen and Johnsen 1982), it is likely to be a combination of these scenarios. Despite these known biases, we did not exclude this early whaling period from the results for several reasons. First, the initial whaling period at South Georgia was close to shore and is documented as plentiful with approximately 100,000 baleen whales caught close to South Georgia prior to 1929 including large numbers of fin and sei whales (Allison 2016). Second, prior to the 1920s, whalers were not using steam-powered capture vessels, and therefore, whaling further offshore in sub-Antarctic waters was unlikely during the initial period. Third, although some variation was observed in spatial distribution of fin and sei whales across time, fin whales were caught throughout the EEZ even during the early period, and sei whales were consistently caught at higher densities in the northern range of the EEZ (Fig. S4). Moreover, whaler preference for specific species shifted throughout the commercial whaling period in the following order: (1st) humpback, (2nd) blue, (3rd) fin, (4th) sei, (5th) minke. Fin whales were the main target between 1937 and 1965, whereas sei whales were the dominant target between 1965 and 1975 (once fin whale abundance had significantly diminished, Tønnessen and Johnsen (1982), pp.164–165). Fin whales were caught throughout the EEZ despite being targeted prior to sei whales, suggesting whaling was already occurring across the entire EEZ before the majority of sei whaling occurred; therefore, we assume here that later

catches were not strongly biased by whaler presence and that the whaling catches reported across the EEZ in summary provide a good indication of feeding ground distribution of sei and fin whales at SGSSI during the twentieth century.

Conclusion

Fin and sei whales co-occurred at South Georgia and the South Sandwich Islands (SGSSI) during the twentieth-century whaling period predominantly during late summer and early autumn. Here, we have provided the first isotopic information for fin and sei whales in this region and by combining isotopic evidence with spatiotemporal information from whaling catch data we show evidence of potential resource partitioning during the commercial whaling period, an era when whale numbers were much higher (Rocha et al. 2015) and competition for resources potentially heightened. Temporal and spatial variation in whaling catches suggests spatiotemporal differences in habitat use of fin and sei whales at SGSSI with the highest numbers of sei whales occurring later in the season and utilising the northern part of the exclusive economic zone compared with fin whales, with both species found nearshore and offshore. Although sample sizes were small, stable isotope analysis of baleen plates suggest limited interspecific overlap in isotopic niches indicative of resource partitioning. Sequential $\delta^{13}\text{C}$ values of baleen plates provide evidence of individuals from both species foraging at lower latitudes prior to arrival at SGSSI during the twentieth-century whaling period. Further dietary and isotopic information (e.g. from baleen of deceased strandings or live skin biopsies) in present-day fin and sei whale populations are needed to understand the various roles these whales play in the SGSSI ecosystem, including any overlap that may occur with neighbouring marine predators, and commercial fisheries.

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Author contributions DLB, JAJ, TCO and AM contributed to study concepts and design. DLB, EH and RHYL performed laboratory analysis and data collection. DLB performed the analysis, prepared the figures and wrote the manuscript. JAJ contributed to manuscript preparation. All authors critically reviewed the results and approved the final version of the manuscript.

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Data availability The data sets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest All the authors declare that they have no conflict of interest.

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study because all experimental work was conducted on whale baleen material that was discarded at sites in South Georgia during the commercial whaling era. Material was transported to the UK by individual researchers prior to the international agreement for CITES regulation of shipment of whales. CITES was adopted by the UK in 1976, and whales were listed under Appendix I of CITES between 1975 and 1986.

Consent to participate Not applicable.

Consent for publication Not applicable.

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